THE LINKAGE RELATIONS BETWEEN THE FACTORS FOR TUNICATE EAR AND STARCHY-SUGARY ENDOSPERM IN MAIZE[1]

W. H. EYSTER

University of Missouri, Columbia, Missouri

Received December 10, 1920

TABLE OF CONTENTS

INTRODUCTION 209
Previous linkage studies in maize 210
Materials and methods 211
Terminology 212
Tunicate character 213
Linkage between tunicate-ear and sugary-endosperm factors 213
Variation in linkage 215
Linkage tests between the T_u–S_u group and other groups of linked factors 217
Linkage tests between the T_u–S_u group and factors whose linkage relations are not yet definitely established 228
SUMMARY 237
LITERATURE CITED 239

INTRODUCTION

At the time the present study was begun more than thirty mutant factors in the corn plant were being investigated, but a surprisingly small number of groups of linked factors had been found. It was, therefore, decided to make a systematic search for linkages by testing each factor in relation to all of the other factors. In this paper are given the results of tests made with tunicate ear, T_u t_u, which was chosen as being especially adapted for such a linkage study. In using tunicate ear, a dominant character, it is not necessary to grow F_2 populations to get the recessives to be used in back-crossing the F_1 plants, as any non-tunicate plant recessive for one or more of the other factors involved in the original cross is a double, triple, or multiple recessive.

The original purpose of this investigation was to establish the linkage relations between the factor pair for tunicate ear, T_u t_u, and other mutant factors in maize. Later, when it was shown by JONES and GALLASTEGUI

[1] Paper number 85, Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, New York.

(1919) that the factor pair for sugary endosperm, S_u s_u, is linked with the factor pair for tunicate ear, T_u t_u, this study was extended to include linkage tests involving sugary endosperm and the other mutant characters. At that time all of the material in the cultures of Dr. R. A. EMERSON and Dr. E. G. ANDERSON that was concerned with the linkage relations of sugary endosperm was transferred to the writer. Some of the tests were made by them and the data are entirely theirs. This fact will be indicated as the data are presented.

PREVIOUS LINKAGE STUDIES IN MAIZE

COLLINS and KEMPTON (1912) were the first to record a case of linkage in maize. They presented data which show a linkage between waxy endosperm and aleurone color, although they did not determine which of the aleurone color factors is concerned. BREGGER (1918) reported further evidence on this linkage and showed clearly that it is the *C* aleurone color factor (EAST and HAYES 1911; EMERSON 1918) that is linked with waxy endosperm. More recently KEMPTON (1919) published data which give additional evidence of the linkage between waxy endosperm and aleurone color. HUTCHISON (1921) has shown that a recessive factor for shrunken endosperm, s_h, and the dominant aleurone color inhibitor, *I*, are also members of this linkage group.

LINDSTROM (1917) reported the second linkage in maize. He found that the factor pair for golden plant, *G g*, is linked with the *R r* aleurone factor pair. In a later paper LINDSTROM (1918) presented additional data on this linkage and gave evidence that a second chlorophyll factor pair, *L l*, which produces yellow seedlings when recessive, is also linked with the *R r* factor pair.

The third linkage recorded in maize was discovered by JONES and GALLASTEGUI (1919) who observed that, when the seeds with starchy and sugary endosperm from a self-pollinated plant heterozygous for both tunicate ear and sugary endosperm were planted separately, the starchy seeds produced a great excess of tunicate plants while the sugary seeds, on the other hand, produced an excess of non-tunicate plants.

It has long been known by EMERSON (1921) that one of the factor pairs for yellow endosperm is linked with the factor pair concerned in the production of purple anthers, P_l p_l.

The factor pair concerned in the production of sun-red plants, *B b*, has been shown by EMERSON (1921) to be linked with the factor pair for liguleless leaf, L_g l_g. More recently EMERSON (1920) found that another mutant

factor pair, T_e t_e, which produces a wholly pistillate plant when recessive, is linked with the factors for sun-red plant color and liguleless leaf. This type of pistillate plant is known as tassel ear.

EMERSON (1920) has found a second type of pistillate plant which he calls tassel seed (T_s t_s). He has shown that tassel seed is wholly different from tassel ear and that it is inherited independently of it. Tassel seed is closely linked with the factor pair for pericarp color, P p.

MATERIALS AND METHODS

The pedigree cultures with which this study was begun were kindly furnished by Dr. R. A. EMERSON. Some of the original crosses were made by him in the summer of 1916. These, together with additional material, were transferred to the writer in the spring of 1917. In the course of this study Dr. EMERSON was exceedingly liberal in furnishing material and gave many valuable criticisms and suggestions so that I am especially indebted to him. My constant association with Dr. ANDERSON was also extremely helpful. Both EMERSON and ANDERSON placed freely at my disposal pedigreed plants involving a number of mutant factors, thus making it possible to get a large amount of linkage data from a minimum number of plants. Data on the linkage relations of sugary endosperm with other mutant factors that are from the notes of EMERSON and ANDERSON will be indicated in the tables by prefixing to the pedigree numbers a distinguishing letter. The letter "E" signifies that the data are from the notes of Dr. EMERSON, and the letter "A" refers in like manner to Dr. ANDERSON.

Ordinary cultural methods were used in growing the plants. The seeds were planted in rows with one seed at a place so that notes could be taken on individual plants. In noting the tunicate character although it is nearly always possible to identify the plants by the long glumes and thick tassels, in every case the husks were torn back and the ear examined for the tunicate character.

Back-cross data are used in every test except for the factor pairs for white seedling, W w, which is lethal when homozygous recessive, and virescent-white seedling, V v, which produces white to yellowish-white seedlings when recessive. A few of the virescent-white seedlings become green and survive, but most of them die in the seedling stage (LINDSTROM 1918).

The probable errors of the ratios were read directly from probable error tables available in the laboratories of the Department of Plant Breeding, CORNELL UNIVERSITY. The probable significance of the deviations in

relation to their probable errors are from the table of PEARL and MINER (1914).

TERMINOLOGY

The following factors were used in the linkage tests reported in this paper:

A a, factor pair for anthocyanin pigmentation in the leaves, sheathes, and husks, and for colored aleurone (EMERSON 1918, 1921).

A_n a_n, factor pair for semi-dwarf plant with anthers on the ears.

B b, factor pair for brown plant color (EMERSON 1921).

B_l b_l, factor pair for brown blotches on the leaves.

C c, factor pair for colored aleurone (EAST and HAYES 1911; EMERSON 1918).

C_r c_r, factor pair which produces a crinkling of the leaves.

D d, factor pair for dwarf plant.

F f, factor pair for a fine striping in the leaves (LINDSTROM 1918).

F_l f_l, factor pair for floury endosperm (EAST and HAYES 1915).

G g, factor pair for golden plant (LINDSTROM 1918).

G_s g_s, factor pair for green striping of the leaves (LINDSTROM 1918).[2]

I i, factor pair which inhibits the production of aleurone color (EAST and HAYES 1911; EMERSON 1918).

J j, factor pair for *japonica* striping of the leaves (LINDSTROM 1918).

L l, factor pair for yellow seedling (LINDSTROM 1918).

L_g l_g, factor pair for leaves without ligules (EMERSON 1912).

P p, factor pair for colored pericarp (EMERSON 1911).

P_l p_l, factor pair for purple anthers (EMERSON 1921).

P_r p_r, factor pair which produces purple aleurone in the presence of the other aleurone factor pairs (EMERSON 1918).

R r, factor pair for red aleurone (EAST and HAYES 1911; EMERSON 1918, 1921).

R_a r_a, factor pair for *ramosa* ear (GERNERT 1912).

S_h s_h, factor pair for shrunken endosperm (HUTCHISON 1921).

S_u s_u, factor pair for sugary endosperm (CORRENS 1901; EAST and HAYES 1911).

T_e t_e, factor pair for pistillate plant, tassel ear (EMERSON 1920).

T_s t_s, factor pair for pistillate plant, tassel seed (EMERSON 1920).

[2] LINDSTROM used the symbol S_l for this factor but G_s is now being used by him and other workers in corn as being the more significant symbol.

T_u t_u, factor pair for tunicate ear (COLLINS 1917).
W w, factor pair for white seedling (LINDSTROM 1918).
W_x w_x, factor pair for waxy endosperm (COLLINS and KEMPTON 1913; BREGGER 1918; KEMPTON 1919).
Y y, one of the factor pairs concerned in the production of yellow endosperm (EAST and HAYES 1911; EMERSON 1921).

TUNICATE CHARACTER

The tunicate plants used in this study were all from a common source, having been obtained by Dr. EMERSON from the Department of Farm Crops, CORNELL UNIVERSITY. The plants resembled sufficiently the strain of tunicate plants described and illustrated by COLLINS (1917) as to make a detailed description here unnecessary. The most important characteristic of tunicate plants is that the glumes of the ear develop to such an extent that each kernel is entirely enclosed. The tassel glumes are also longer than those of non-tunicate plants and this gives the tassels a thickened appearance. It is possible to identify tunicate plants by their thickened tassels.

COLLINS (1917) found that the homozygous tunicate plants are sterile and that the ordinary type of tunicate plants is a case of imperfect dominance somewhat analogous to the blue Andalusian fowl. JONES and GALLASTEGUI (1919) reported observations on the inheritance of the tunicate character which confirm the conclusions of COLLINS.

A summary of the back-crosses made in the course of this study shows that of the 12,324 plants noted, 6113 were tunicate and 6211 were non-tunicate. This is a deviation from the 1:1 ratio expected, of 49.0 ± 37.4 plants. A deviation as large as this would be expected to occur about 38 times out of every 100 trials due to the errors of random sampling. These data give further evidence of COLLINS's interpretation.

LINKAGE BETWEEN TUNICATE EAR AND SUGARY ENDOSPERM FACTORS

Attention has already been called to the paper by JONES and GALLASTEGUI (1919) in which it is shown that the factor pair for tunicate ear, T_u t_u, is linked with the factor pair for sugary endosperm, S_u s_u. The numbers from which this observation was made are small, yet the distribution is clearly different from the ordinary dihybrid ratio which would obtain if the factors assorted independently.

A number of crosses were made between heterozygous tunicate plants with homozygous starchy endosperm and non-tunicate plants with sugary

endosperm. The resulting seeds were all starchy. A small planting was made from each cross and the progenies consisted of tunicate plants and non-tunicate plants in approximately equal numbers. Tunicate plants of these progenies, which had the genetic constitution $T_u\ t_u\ S_u\ s_u$, were back-crossed reciprocally with non-tunicate plants homozygous for sugary endosperm. The results of these back-crosses are given in table 1. The starchy and sugary seeds from these back-crossed ears were planted separately. The starchy seeds in every instance produced an excess of tunicate plants and the sugary seeds produced an excess of normal plants. The parental combinations of these factors tend to be inherited together with a recombination occurring in about 27 percent of the cases in the megasporocytes, and approximately 35 percent in the microsporocytes. The tendency of

TABLE 1

Progenies from back-crosses involving tunicate ear and sugary endosperm.

PEDIGREE NUMBERS	$S_u\ T_u$	$S_u\ t_u$	$s_u\ T_u$	$s_u\ t_u$	PERCENT CROSSING OVER
$T_u\ t_u\ S_u\ s_u \times t_u\ t_u\ s_u\ s_u$					
196–10 × 192–4	89	19	31	98	21.10
198–9 × 192–3	147	57	63	127	30.46
140–4 × E7595–11	90	35	24	70	26.94
Totals	326	111	118	295	26.94
$t_u\ t_u\ s_u\ s_u \times T_u\ t_u\ S_u\ s_u$					
E7595–11 × 140–4	26	8	19	25	34.62
E8575–4 × 201–7	78	56	32	86	34.92
Totals	104	64	51	111	34.85

these factors to remain together in inheritance can be explained by assuming that they are located in the same chromosome and that the recombinations are the result of crossing over. In megasporogenesis the amount of crossing over in the plants tested varied from 21.1 to 30.5 percent while in microsporogenesis the amount of crossing over in both plants tested was approximately the same, though about 8 percent higher than in megasporogenesis.

The data reported by JONES and GALLASTEGUI (1919), with only about 8 percent of crossing over, indicate a much closer linkage between the factors for tunicate ear and sugary endosperm than is shown by any of the back-cross data here presented. These investigators call attention to the fact that the plants from which their data were taken were grown in hills, and that when classifying them it was not always possible to tell which was plant and which was sucker as the plants suckered profusely. It is not

impossible that the same plants may have been counted more than once. Whether this source of error together with the small number of F_2 plants grown by them is sufficient to account for the difference between their results and the results of this study, or whether this wide variation in linkage is due to other causes, is not known.

VARIATION IN LINKAGE

These data indicate that crossing over is not absolutely fixed in amount, but varies, due apparently to fluctuations in environmental conditions, or to internal changes in the mechanism of crossing over itself. MORGAN (1919) has recently given a summary of the variation in crossing over in *Drosophila melanogaster*. It has been found that in this organism crossing over is affected both by environmental conditions and genetical factors carried by the chromosomes themselves. In plants crossing over occurs in the production of both megaspores and microspores and apparently more frequently in the latter.

TABLE 2

Statistical study of Altenburg's data on Primula sinensis. After GOWEN (1919).

	MALE HETERO-ZYGOUS	FEMALE HETERO-ZYGOUS	MALE PERCENT	FEMALE PERCENT	DIFFERENCE	DIFF / P. E. Diff.
Non-crossovers	1829	266	55.56	67.81	12.30±1.7	7.2
First single	1053	107	31.97	27.30	4.69±1.4	3.2
Second single	325	11	9.87	2.81	7.07±0.9	7.4
Double	85	8				

ALTENBURG (1916) published back-cross data on factor linkages in *Primula sinensis*, which indicate that crossing over in microsporogenesis is consistently higher than in megasporogenesis. GOWEN (1919) made a statistical study of ALTENBURG'S data, a summary of which is given in table 2. The deviations range from 3.2 to 7.4 times as large as their probable errors. GOWEN points out that deviations as large as these are not without significance.

The writer has made a similar statistical study of differences in the amount of crossing over in the microsporocytes and megasporocytes in maize with the results shown in table 3. The data reported in this paper on the relation between tunicate ear and sugary endosperm indicate that the average amount of crossing over in the microsporocytes is 7.9 ± 2.0 percent higher than in the megasporocytes. The odds against a deviation as great as this being due to the errors of random sampling are about 135 to 1, and may be considered significant. A summary of BREGGER'S (1918)

data on the linkage between waxy endosperm and the *C* aleurone factor shows that crossing over was 2.46 ± 1.11 percent higher in microsporogenesis than in megasporogenesis. In this case the deviation is approximately twice as large as the probable error. A difference of this magnitude would be expected about once in five trials due to errors of random sampling and is usually considered not significant. It is important to note, however, that it is in microsporogenesis that the higher percentage of crossing over occurs. The plants heterozygous for waxy endosperm and the *C* aleurone factor were grown by BREGGER in the summer of 1916 while the plants heterozygous for tunicate ear and sugary endosperm were grown in the summer of 1918, and in a different part of the garden. It

TABLE 3

Variation in linkage in maize.

FACTORS INVOLVED	FEMALE HETERO-ZYGOUS	MALE HETERO-ZYGOUS	FEMALE PERCENT	MALE PERCENT	DIFFERENCE	DIFF. / P. E. Diff.
T_u–s_u						
Non-crossovers	621	215	73.06	65.15	7.91±1.99	3.97
Crossovers	229	115	26.94	34.85		
C–w_z						
Non-crossovers	1445	832	74.25	71.78	2.46±1.11	2.22
Crossovers	501	327	25.75	28.22		

TABLE 4

	S_u T_u	S_u t_u	s_u T_u	s_u t_u	PERCENT CROSSOVERS
t_u t_u s_p s_u × T_u t_u S_u s_u					
E8575–4 × 140–4	26	8	19	25	34.6±3.8
T_u t_u S_u s_u × t_u t_u s_u s_u					
140-4 × E8575–4	90	35	24	70	26.9±2.7
Difference					7.7±4.4

is evident that the environmental conditions were different for these two lots of plants. Neither can the plants which were grown the same season be considered to have been exposed to identical environmental conditions, as the seeds were planted without regard to soil differences. Whether this variation in linkage is due to environmental conditions or to genes in the chromosomes themselves is at present not known.

Perhaps the best measure of the difference in the amount of crossing over in the microsporocytes and megasporocytes could be obtained by testing both the pollen and ovules of individual plants. Incidentally one plant heterozygous for tunicate ear and sugary endosperm was tested in this manner. The pedigree number of this plant is 140-4. Plant E8575-4

was of the genetic constitution $t_u\ t_u\ s_u\ s_u$ and was used to test the pollen and ovules of plant 140-4. The reciprocal crosses of these plants are given in table 4. It is seen that crossing over was 7.7 ± 4.4 percent higher in the microsporocytes than in the megasporocytes. Unfortunately the number of plants grown from these back-crosses is small.

LINKAGE TESTS BETWEEN THE T_u-s_u GROUP AND OTHER GROUPS OF LINKED FACTORS

Tests involving T_u and s_u with the C-w_z-s_h-I group

Factors T_u and C

Plants heterozygous for tunicate ear and sugary endosperm were back-crossed to C aleurone testers of the constitution $A\ A\ c\ c\ R\ R\ t_u\ t_u$. The progenies from these back-crosses are given in table 5. The deviation from the 1:1 ratio expected for independent inheritance is only 1.0 ± 10.1 plants which is a very close fit.

TABLE 5

Progeny from the back-cross $T_u\ t_u\ C\ c \times t_u\ t_u\ c\ c$.

PEDIGREE NUMBERS	$S_u\ T_u$	$S_u\ t_u$	$s_u\ T_u$	$s_u\ t_u$
362–365	31	32	36	36
366–367	67	64	83	84
368–369	53	53	54	58
370–371	54	68	60	69
Totals	205	217	233	247

Factors S_u and C

Extensive tests have been made by EMERSON and ANDERSON between starchy-sugary endosperm and the C aleurone factor. Heterozygous plants from the cross $S_u\ S_u\ C\ C \times s_u\ s_u\ c\ c$ were back-crossed to sugary C testers of the constitution $A\ A\ c\ c\ R\ R\ s_u\ s_u$. The plants grown from these back-crosses are given in table 6 under coupling series. This represents a coupling series as both dominant factors were associated in one of the parental plants. In the second part of table 6 are given the results of back-crossing heterozygous plants from the cross $S_u\ S_u\ c\ c \times s_u\ s_u\ C\ C$ to sugary C testers. As each parent contributed one of the dominant factors these data may be considered a repulsion series. In the coupling series there was a total of 2335 seeds. Of these 1185 had the parental combina-

tion and 1150 the new combinations of the factors, a deviation of 17.5 ± 16.3 from the 1:1 ratio expected. There was a total of 2067 seeds in the repulsion series of which 1027 had the parental combinations while 1040 had the factors in new combinations. This is a deviation from a 1:1 ratio of only 6.5 ± 15.3. In both cases the fit is very close.

TABLE 6

Progeny from the back-cross $S_u\ s_u\ C\ c \times s_u\ s_u\ c\ c$.

PEDIGREE NUMBERS	$C\ S_u$	$C\ s_u$	$c\ S_u$	$c\ s_u$
Coupling series				
E7689-2 × E7509-6	115	82	117	84
E4734-13 × E4717-32	58	54	53	48
E8566-15 × E8479-1	91	127	101	134
E8566-7 × E8479-1	113	121	103	137
E7507-10 × A196-1	33	31	41	36
E7507-2 × A438-5	97	96	81	120
E8610-2 × E8567-1	65	72	71	54
Totals	572	583	567	613
Repulsion series				
E2878-1 × E2884-50	28	14	26	28
E2879-4 × E2884-68	34	23	16	24
E2881-4 × E2884-64	17	23	18	16
E2882-6 × E2884-43	96	66	74	62
E2882-9 × E2884-36	41	42	38	50
E2882-2 × E2884-43	66	39	95	28
E2883-7 × E2885-6	85	71	86	106
E8611-1 × E8567-1	88	97	85	90
E8611-3 × E8567-4	87	101	113	94
Totals	542	476	551	498

Factors T_u and W_z

A plant homozygous for waxy endosperm was crossed with a heterozygous tunicate plant with starchy endosperm. All of the resulting seeds were starchy, which, when planted produced tunicate and non-tunicate plants in approximately equal numbers. One of the tunicate plants of this progeny was back-crossed to a normal plant with waxy endosperm. The ear produced from this cross contained 104 starchy and 107 waxy seeds. These seeds were planted separately the following year but the germination was exceedingly poor. None of the waxy and only a small percentage of the starchy seeds produced plants. Of the 18 plants grown, 8 were tunicate and 10 normal.

Factors T_u and S_h

It was observed that the back-crossed ear in the tunicate-waxy test also segregated for shrunken endosperm. Of the 104 starchy seeds, 34 were noted as shrunken and 70 as normal. Of the 107 waxy seeds 80 were shrunken and only 27 were normal non-shrunken. Because of the immaturity of the seeds their separation into the various classes was not altogether satisfactory, but the numbers are distinctly different from the 1:1:1:1 ratio expected in independent inheritance. These data indicate a linkage between waxy endosperm and shrunken endosperm with about 29 percent of crossing over. The shrunken and normal seeds were planted separately. From the normal seeds there were produced 5 tunicate plants and 7 normal plants and from the shrunken seeds there were 3 tunicate plants and 3 normal plants.

Factors S_u and I

Several plants heterozygous for the factor pairs for starchy-sugary endosperm and the dominant aleurone color inhibitor were back-crossed by ANDERSON to plants having sugary endosperm and recessive for the aleurone-color inhibitor. The progenies from these back-crosses are given in table 7. There were 340 kernels with factors combined as in the parents and 310 kernels with the recombination of the factors. The deviation from a 1:1 ratio is 15.0 ± 8.6.

TABLE 7

Progeny from the back-cross, $S_u\ s_u\ I\ i \times s_u\ s_u\ i\ i$

PEDIGREE NUMBERS	$S_u\ I$	$s_u\ I$	$S_u\ i$	$s_u\ i$
A890–8 × A889–4	34	14	36	29
A890–9 × A888–4	79	58	77	58
A891–7 × A888–2	75	56	69	65
Totals	188	128	182	152

So far as tests have been made the data indicate that the factors for tunicate ear and sugary endosperm are inherited independently of the factors belonging to the *C-W_x-S_h-I* linkage group.

Tests involving T_u and S_u with the G-R-L group

Factors T_u and G

Back-crosses involving tunicate ear and golden plant gave a total of 349 green and 314 golden plants as shown in table 8. Of the green plants

173 were tunicate and 176 non-tunicate, a fairly good 1:1 ratio. Of the golden plants 147 were tunicate and 167 non-tunicate, also a fair approximation to the equality expected. Classes one and four, which represent

TABLE 8

Progeny from the back-cross $T_u\ t_u\ G\ g \times t_u\ t_u\ g\ g$

PEDIGREE NUMBERS	$G\ T_u$	$G\ t_u$	$g\ T_u$	$g\ t_u$
406	47	40	39	46
407	31	30	15	23
408	74	76	62	63
90	21	30	31	35
Totals	173	176	147	167

the parental combinations of the factors, have a total of 340 plants while classes two and three, with the new combinations of the factors, have a total of 323 plants. The deviation from the 1:1 ratio expected in independent inheritance is 8.5 ± 8.6. A deviation as large as this would be expected once in every two trials.

Factors T_u and R

A number of plants heterozygous for tunicate ear and the R aleurone factor were back-crossed to R aleurone testers of the constitution $A\ A\ C\ C\ r\ r\ t_u\ t_u$. The progenies of these back-crosses are given in table 9.

TABLE 9

Progeny from the back-cross $T_u\ t_u\ R\ r \times t_u\ t_u\ r\ r$

PEDIGREE NUMBERS	$R\ T_u$	$R\ t_u$	$r\ T_u$	$r\ t_u$
429–430	4	4	2	1
431–433	54	52	43	45
434–436	56	62	58	72
437–438	39	50	46	51
Totals	153	168	149	169

Colored and colorless seeds in approximately equal numbers were produced as expected. From the colored seeds 321 plants were grown, of which 153 were tunicate and 168 non-tunicate. The colorless seeds produced 149 tunicate and 169 non-tunicate plants. In each case the ratios are fairly close to the equality expected. Of these progenies 322 plants had the factors in the same combinations as the parents and 317 plants were the result of the new combinations of the factors involved. This is a deviation

from the 1:1 ratio expected of 2.5 ± 8.5 plants, which is an exceedingly close fit.

Factors S_u and R

A number of back-crosses involving sugary endosperm and the R aleurone factor were made by EMERSON and ANDERSON. The progenies of these back-crosses are given in table 10. The back-crossed ears produced a total of 1610 starchy and 1368 sugary seeds. The starchy seeds were

TABLE 10

Progeny from the back-cross $S_u\ s_u\ R\ r \times s_u\ s_u\ r\ r$

PEDIGREE NUMBERS	$S_u\ R$	$S_u\ r$	$s_u\ R$	$s_u\ r$
E2878–1 × E2884–50	21	31	46	24
E2879–4 × E2884–68	22	17	19	23
E2882–6 × E2884–43	91	76	47	66
E2882–9 × E2884–36	30	36	34	30
E2882–2 × E2884–43	68	54	13	28
E6653–2 × E6652–4	17	12	4	6
E6653–7 × E6652–3	82	75	57	69
E2883–7 × E2885–6	19	43	17	30
A273–7 × E7507–9	47	62	37	33
A273–10 × E7507–7	25	26	26	19
A266–4 × A273–7	29	29	2	3
E8483–5 × E8767–4	58	37	49	40
E8483–6 × E8572–4	42	28	32	28
E8578–1 × E8483–3	75	72	89	94
E8578–15 × E8483–2	62	64	75	71
E8611–9 × E8575–4	89	106	91	105
E8611–4 × E8575–4	28	37	27	34
Totals	805	805	665	703

colored and colorless in an exactly 1:1 ratio, there being 805 of each. Of the sugary seeds, 665 were colored and 703 colorless, a fairly close approximation to a 1:1 ratio. Of the total number of seeds 1508 had the factors combined as in the parents and 1470 had the factors in the new combinations. This is a deviation from the 1:1 ratio expected of only 19.0 ± 18.4 individuals. A deviation as great as this would be expected to occur once in every two trials due to the errors of random sampling.

The data from these tests give no indication of a linkage between either T_u or S_u and the members of the *G-R-L* linkage group.

Tests involving T_u and S_u with the B-L_9-T_e group

Factors T_u and B

A number of sun-red plants of the constitution T_u t_u B b were back-crossed to dilute sun-red plants with the factorial constitution t_u t_u b b. These back-crosses gave a total of 1405 plants as shown in table 11. Of these 692 had the parental combinations of the factors while the two new classes resulting from the recombination of factors had a total of 713 plants. This is a deviation of 10.5 ± 12.6 from a 1:1 ratio expected for factors that are inherited independently of each other.

TABLE 11

Progeny from the back-cross T_u t_u B b × t_u t_u b b.

PEDIGREE NUMBERS	B T_u	B t_u	b T_u	b t_u
362–365	30	28	37	30
366–367	70	71	80	76
126	8	3	3	4
424–426	83	56	84	94
406	33	40	34	18
408	23	14	25	29
93	15	14	21	9
449–450	40	21	48	12
460–463	51	75	59	67
Totals	353	322	391	339

Factors S_u and B

Other sun-red plants known to be heterozygous for the factor pairs B b and S_u s_u were back-crossed by EMERSON and ANDERSON to plants having the genetic constitution s_u s_u b b. The results of these back-crosses are given in table 12. Starchy and sugary seeds were produced in approxi-

TABLE 12

Progeny from the back-cross S_u s_u B b × s_u s_u b b.

PEDIGREE NUMBERS	S_u B	S_u b	s_u B	s_u b
E8214–E8217	36	39	17	17
E8218–E8221	45	65	34	33
E8222–E8225	54	36	18	15
E7347–E7348	69	88	57	69
A793–A796	75	89	61	57
Totals	279	317	187	191

mately equal numbers. From the table it may be seen that the sugary seeds produced only 378 plants while the starchy seeds produced 596 plants. This difference is due to the much lower percentage of germination of the sugary seeds. Both starchy and sugary seeds gave sun-red and green plants in fairly equal numbers. Of these plants 470 had the parental combinations of the factors and 504 the factors in the new combinations. This is a deviation of 17.0 ± 10.4 from equality expected for independently inherited factors.

Factors T_u and L_g

Many of the back-crosses made in the course of this study involved tunicate ear and liguleless leaf. Some of these back-cross progenies are given in table 13. There is a total of 1692 plants and for every class the

TABLE 13

Progeny from the back-cross $T_u\ t_u\ L_g\ l_g \times t_u\ t_u\ l_g\ l_g$.

PEDIGREE NUMBERS	$L_g\ T_u$	$L_g\ t_u$	$l_g\ T_u$	$l_g\ t_u$
494	43	49	50	35
496	28	20	21	19
495	58	59	73	61
492	7	10	7	6
493	14	16	7	13
489	18	33	34	32
491	20	25	22	14
490	59	45	62	67
488	26	48	33	41
418	8	11	6	16
419	5	4	5	3
372	91	75	65	76
373–374	17	5	9	7
375	34	28	31	21
Totals	428	428	425	411

observed number is very close to the number expected for independent inheritance. There were 839 plants with the parental combinations and 853 with the new combinations of these factors. This is a deviation of 7.0 ± 13.9 from the 1:1 ratio expected. This is a close fit and indicates that these factor pairs are not linked.

Factors S_u and L_g

Several tests between the factor pairs $S_u\ s_u$ and $L_g\ l_g$ were made by EMERSON and ANDERSON. The progenies of these back-crosses are listed in

table 14. The starchy seeds produced 683 plants with normal leaves and 652 plants with leaves without ligules. The sugary seeds produced 376 plants with normal leaves and 379 plants with liguleless leaves. In each case the numbers closely approach the 1:1 ratio expected. Of the total number of plants 1062 had the same combinations of these factors as the parents and 1028 were the result of the new combinations of factors. This is a deviation of only 17.0 ± 15.4 from equality and apparently the factors for sugary endosperm and liguleless leaf are not linked.

TABLE 14

Progeny from the back-cross $S_u\ s_u\ L_g\ l_g \times s_u\ s_u\ l_g\ l_g$.

PEDIGREE NUMBERS	$S_u\ L_g$	$S_u\ l_g$	$s_u\ L_g$	$s_u\ l_g$
A395–1 × E7317–6	90	77	61	70
A395–8 × E7317–2	20	25	27	21
A395–9 × E7317–5	111	95	89	79
E7317–6 × E7318–4	61	63	40	40
E7318–4 × E7317–6	84	81	56	47
E7318–1 × E7317–4	63	58	36	38
E7316–4 × E7317–5	30	28	9	6
E7316–5 × E7317–5	32	25	7	13
E7316–6 × E7317–5	65	52	15	26
E7316–6 × E7322–4	34	44	7	7
E7322–4 × E7317–6	30	32	5	4
E7322–3 × E7317–4	63	72	24	28
Totals	683	652	376	379

The data from these tests indicate that tunicate ear and sugary endosperm are inherited independently of the *B-L$_g$-T$_e$* linkage group.

Tests involving T_u and S_u with the P-T$_e$ group

Factors S_u and P

Several plants heterozygous for starchy-sugary endosperm and pericarp color from the cross $S_u\ S_u\ P\ P \times s_u\ s_u\ p\ p$ were back-crossed by EMERSON and ANDERSON to plants with sugary endosperm and colorless pericarp. The progenies of these back-crosses are given in table 15. From the starchy seeds were grown 417 plants. Of these 205 had colored and 212 colorless pericarp which approaches closely a 1:1 ratio. Of the 289 plants grown from the sugary seeds 144 had colored and 145 colorless pericarp which is almost exactly a 1:1 ratio. There was a total of 350 individuals with the parental factor combinations and 356 with the factors in new combinations. This is a deviation of only 3.0 ± 9.0 from equality and indicates that these factor pairs are inherited independently.

TABLE 15

Progeny from the back-cross $S_u\ s_u\ P\ p \times s_u\ s_u\ p\ p$.

PEDIGREE NUMBERS	$S_u\ P$	$S_u\ p$	$s_u\ P$	$s_u\ p$
E6653–2 × E6652–4	15	12	6	3
A395–1 × E7317–60	75	78	56	72
A395–8 × E7317–2	25	20	20	28
A395–9 × E7317–5	90	102	62	42
Totals	205	212	144	145

Factors T_u and P

A number of crosses made for other tests involved tunicate ear and variegated pericarp color and a few of such heterozygous plants were back-crossed with non-tunicate plants having colorless pericarp. From these back-crossed ears were grown 1194 plants and of these 582 were tunicate and 612 non-tunicate, as shown in table 16. The tunicate plants were not noted for pericarp color as the variegation is sometimes limited to a few seeds, or even a single seed, and it would have been necessary

TABLE 16

Progeny from the back-cross $T_u\ t_u\ P\ p \times t_u\ t_u\ p\ p$.

PEDIGREE NUMBERS	$T_u\ P + T_u\ p$	$t_u\ P$	$t_u\ p$
488	59	35	50
489	52	21	45
490	121	64	58
491	42	23	22
492	14	5	10
493	21	21	12
494	93	38	48
495	131	56	64
496	49	13	27
Totals	582	276	336

to husk out and examine every seed to make sure that a given ear had colorless and not variegated pericarp. Of the non-tunicate plants 276 were noted as having pericarp color and 336 as having colorless pericarp. This is a deviation of 30.0 ± 8.3 from equality. The separation of the non-tunicate plants into classes with and without pericarp color was made on the plants in the field on a very cold day and it is possible that this wide deviation is due to having noted some of the exceedingly light variegated ears as colorless.

No tests have yet been made involving tunicate ear and sugary endosperm with tassel seed.

Tests involving T_u and S_u with the S_m-Y-P_l group

Factors T_u and P_l

Several plants heterozygous for tunicate ear and the plant-color factor pair, $P_l\ p_l$, were back-crossed to non-tunicate sun-red plants of the genetic constitution $t_u\ t_u\ p_l\ p_l$. The progenies of these back-crosses are given in table 17. The classes representing the parental combinations of these factors include 172 plants, while in the two classes with the new combinations of the factors there are 181 individuals. This is a deviation of only 4.5 ± 6.2 from a 1:1 ratio and indicates the independence of these factor pairs.

TABLE 17

Progeny from the back-cross $T_u\ t_u\ P_l\ p_l \times t_u\ t_u\ p_l\ p_l$.

PEDIGREE NUMBERS	$T_u\ P_l$	$t_u\ P_l$	$T_u\ p_l$	$t_u\ p_l$
397–398	9	14	16	14
421	46	64	59	76
422–423	11	11	11	11
429–430	2	4	2	3
Totals	68	93	88	104

Factors S_u and P_l

A number of plants heterozygous for starchy-sugary endosperm and the purpling plant-color factor pair, $P_l\ p_l$, were back-crossed by EMERSON and ANDERSON to dilute sun-red plants with sugary endosperm. The progenies of these back-crosses consisted of 557 dilute purple and 555

TABLE 18

Progeny from the back-cross $S_u\ s_u\ P_l\ p_l \times s_u\ s_u\ p_l\ p_l$.

PEDIGREE NUMBERS	$S_u\ P_l$	$S_u\ p_l$	$s_u\ P_l$	$s_u\ p_l$
E7317–6 × E7322–4	16	19	2	3
E7322–4 × E7317–6	19	16	4	4
E7322–5 × E7317–4	28	35	19	18
A273–7 × E7507–9	110	105	70	69
A273–10 × E7507–7	55	48	66	70
E7507–2 × A438–5	69	67	71	65
E7509–25 × A273–2	16	17	12	19
Totals	313	307	244	248

dilute sun-red plants. Of these plants 561 had the parental combinations and 551 had the recombinations of the factor pairs involved. This is a deviation of 5.0 ± 11.2 from equality that obtains when the factor pairs are inherited independently. These results are given in table 18.

Tests involving T_u and S_u with the A a factor pair

The factor pair for anthocyanin pigment, *A a*, is concerned in the production of color in the leaves and stem of the corn plant, and also in the production of color in the aleurone grains of its seeds, as shown by EMERSON (1918, 1921). EMERSON and ANDERSON have tested this factor pair with the other groups of linked factors and it seems to be independent of them.

Factors T_u and *A*

A sun-red plant of the genetic constitution T_u t_u *A A* was crossed with a brown plant which had the constitution t_u t_u *a a* (EMERSON 1921). The F_1 plants were all purple as expected. One of these purple plants, heterozygous for tunicate ear and the anthocyanin factor, was back-crossed with a brown non-tunicate plant. In the progeny there were 35 tunicate plants and 39 non-tunicate plants. Eighteen of the tunicate plants were purple and 17 were brown, and of the non-tunicate plants 23 were purple and 16 brown. The numbers are small but they suggest the 1:1 ratio expected for factors that are inherited independently.

Factors S_u and *A*

A plant heterozygous for both sugary endosperm and the *A a* plant- and aleurone-color factor pair was back-crossed by EMERSON to a plant recessive for these factors. The resulting ear contained 149 starchy and 165 sugary seeds. Of the starchy seeds 79 were colored, that is, they carried the *A* factor, and 70 lacked this factor but carried its allelomorph, *a*, and were colorless. In like manner 87 of the sugary seeds were colored and 78 were colorless. There are just as many seeds with the parental combinations of the factors as there are with the factors in the new combinations. It is quite probable that these factors are inherited independently.

LINKAGE TESTS BETWEEN THE T_u-S_u LINKAGE GROUP AND FACTORS WHOSE LINKAGE RELATIONS ARE NOT YET DEFINITELY ESTABLISHED

Tests involving T_u and S_u with anther ear, A_n a_n

Factors T_u and A_n

Several plants heterozygous for tunicate ear and anther ear were back-crossed to non-tunicate anther-ear plants. The progenies of these back-crosses are given in table 19. Of the 464 plants grown, 217 had the parental

TABLE 19

Progeny from the back-cross T_u t_u A_n a_n × t_u t_u a_n a_n.

PEDIGREE NUMBERS	A_n T_u	A_n t_u	a_n T_u	a_n t_u
358	61	92	70	77
359	43	48	29	27
361	5	4	4	4
Totals	109	144	103	108

combinations of the factors, while 247 resulted from the recombinations of the factors. This is a deviation from equality of 15.0 ± 7.3 plants and makes it appear that these factor pairs are inherited independently.

Tests involving T_u and S_u with blotched leaf, B_l b_l

Factors S_u and B_l

Two plants heterozygous for starchy-sugary endosperm and blotched leaf were back-crossed with plants homozygous for sugary endosperm and blotched leaf. As may be seen in table 20 there were 161 plants with the

TABLE 20

Progeny from the back-cross S_u s_u B_l b_l × s_u s_u b_l b_l.

PEDIGREE NUMBERS	S_u B_l	S_u b_l	s_u B_l	s_u b_l
E6653-2 × E6652-4	19	10	5	5
E6653-7 × E6652-3	82	75	71	55
Totals	101	85	76	60

parental combinations and the same number of plants with the factors concerned in the new combinations. These data indicate that these factors are inherited independently. No tests were made involving tunicate ear and blotched leaf.

Tests involving T_u and S_u with crinkly leaf, C_r c_r

Factors T_u and C_r

A number of plants heterozygous for tunicate ear and crinkly leaf were back-crossed to non-tunicate plants with crinkly leaves. The progenies of these back-crosses are given in table 21 where it will be seen that more plants were noted as non-crinkly than as crinkly. This is doubtless due to the fact that often the crinkly character is not very distinct and conse-

TABLE 21

Progeny from the back-cross T_u t_u C_r c_r × t_u t_u c_r c_r.

PEDIGREE NUMBERS	C_r T_u	C_r t_u	c_r T_u	c_r t_u
372	93	82	63	68
375	45	38	20	11
Totals	138	120	83	79

quently some crinkly plants are classed as normal plants. Of the plants classed as normal, 138 were tunicate and 120 non-tunicate. Of those classed as crinkly 83 were tunicate and 79 non-tunicate. In each case the numbers approach a 1:1 ratio. Of the total progeny 217 were noted as having the parental combinations of the factors and 203 as the result of the recombinations of factors. The deviation from equality, which obtains or is approached when factors are independent, is 7.0 ± 6.9 and is considered a good fit.

Factors S_u and C_r

Tests were also made between sugary endosperm and crinkly leaves by EMERSON and the writer. Plants heterozygous for both of these factors were back-crossed with crinkly plants grown from sugary seeds. The progenies of these back-crosses are given in table 22. Fewer plants were classed as crinkly than as normal. Of the 392 plants grown from starchy

TABLE 22

Progeny from the back-cross S_u s_u C_r c_r × s_u s_u c_r c_r.

PEDIGREE NUMBERS	S_u C_r	S_u c_r	s_u C_r	s_u c_r
501–504	50	40	33	25
525–528	64	60	64	34
529–532	96	82	91	66
Totals	210	182	188	125

seeds 210 were noted as normal and 182 as crinkly. The sugary seeds produced 313 plants of which 188 were noted as normal and 125 as crinkly. The total progeny consisted of 705 plants and 335 of them had the parental combination of factors while 370 were noted as having the factors in the new combinations. This is a deviation from equality of 17.5 ± 9.0 and may be considered a good fit. In these tests the data indicate that the factor pair for crinkly leaf does not belong to the T_u-S_u linkage group.

Tests involving T_u and S_u with dwarf plant, D d

Factors T_u and D

A number of back-crosses involving tunicate ear and the plant character called dwarf, *D d*, gave the progenies listed in table 23. Of the 485 plants

TABLE 23

Progeny from the back-cross T_u t_u D d × t_u t_u d d.

PEDIGREE NUMBERS	$D\ T_u$	$D\ t_u$	$d\ T_u$	$d\ t_u$
376	6	10	14	9
377	4	2	1	1
378	6	6	2	2
379	6	8	6	1
380–381	63	53	34	24
382–383	14	18	10	11
384–385	26	21	11	7
388	13	15	7	7
389–390	17	10	2	8
391	6	10	2	2
Totals	161	153	89	72

in these progenies 314 were normal and 171 were dwarf. This very wide deviation from a 1:1 ratio is due to the failure of many dwarf plants to grow to maturity under field conditions. Only under the most favorable conditions is it possible to grow all of the dwarf plants to maturity. The normal plants were tunicate and non-tunicate in approximately equal numbers, there being 161 of the former and 153 of the latter. Of the dwarf plants 89 were tunicate and 72 non-tunicate. This is a rather wide deviation from a 1:1 ratio but the numbers are small. There were 233 plants with the parental combinations and 242 with the recombinations of these factor pairs. This is a deviation of only 4.5 ± 7.3 from a 1:1 ratio, and indicates that the factor pairs for tunicate ear and dwarf plant are not linked.

Tests were also made involving sugary endosperm and dwarf plant but these data are not available at present. The data indicate, however, that sugary endosperm and dwarf plant are inherited independently.

Tests involving T_u and S_u with fine striping, F f

Factors T_u and F

Back-crosses involving tunicate ear and the chlorophyll pattern called fine striping gave the progenies listed in table 24. There was a total of

TABLE 24

Progeny from the back-cross $T_u\ t_u\ F\ f \times t_u\ t_u\ f\ f$.

PEDIGREE NUMBERS	$F\ T_u$	$F\ t_u$	$f\ T_u$	$f\ t_u$
391a	29	34	33	17
391b	24	33	24	19
392	61	48	53	35
393	64	41	55	65
394–395	34	20	23	21
Totals	212	176	188	157

369 plants with the parental combinations and 364 with the recombinations of these factor pairs. This is a deviation of only 2.5 ± 9.1 from the equality expected when the factors tested are not linked.

No tests were made involving sugary endosperm with fine striping.

Tests involving T_u and S_u with floury endosperm, $F_1 f_1$

Factors T_u and F_1

A number of back-crosses involving tunicate ear and floury endosperm gave the results shown in table 25. Both horny and floury seeds were

TABLE 25

Progeny from the back-cross $T_u\ t_u\ F_1\ f_1 \times t_u\ t_u\ f_1\ f_1$.

PEDIGREE NUMBERS	$F_1\ T_u$	$F_1\ t_u$	$f_1\ T_u$	$f_1\ t_u$
397–398	20	21	3	9
399–403	24	24	18	20
404–405	12	22	21	26
Totals	56	67	42	55

produced on tunicate and non-tunicate plants in approximately equal numbers. The two classes having the parental combinations of these

factor pairs include 111 plants and the classes with the factor recombinations have a total of 109 plants. This is a deviation of only 1.0 ± 5.0 from a 1:1 ratio and indicates that these factor pairs are inherited independently.

No tests were made involving sugary endosperm with floury endosperm.

Tests involving T_u and S_u with japonica striping, J j

Factors T_u and J

A number of plants heterozygous for tunicate ear and the *japonica* chlorophyll pattern (LINDSTROM 1918) were back-crossed with non-tunicate, *japonica*-striped plants. The progenies from these back-crosses are given in table 26. Of the total 341 plants were classed as green and 234 as *japonica*-striped. This deficiency in *japonica* plants is doubtless due to the fact that in some plants the *japonica* character is so much reduced that it is represented by a mere line or splash and such plants are easily overlooked, and classed as green. It is possible that in taking these data some of the plants were inconspicuously striped and were noted as green. Both green and *japonica* plants show a good 1:1 ratio of tunicate and non-tunicate plants. Of the total progenies 293 plants had the parental combinations of the factor pairs and 282 resulted from factor recombinations. This is a deviation of 5.5 ± 8.1 from equality and indicates that tunicate ear and *japonica* striping are inherited independently.

Tests involving sugary endosperm and *japonica* striping were not made.

Tests involving T_u and S_u with purple aleurone, P_r p_r

Factors T_u and P_r

Two plants heterozygous for tunicate ear and purple aleurone were back-crossed with non-tunicate plants with homozygous red aleurone. Ears were produced with purple and red seeds in approximately equal numbers. From the purple seeds were grown 72 tunicate and 70 non-tunicate plants and from the red seeds 80 tunicate and 70 non-tunicate plants were produced, a good 1:1 ratio in each case. Of the total progenies 142 had the parental combination of factors and 150 the factors in recombinations. This is a deviation of 4.0 ± 5.8 from equality and indicates factor independence.

Factors S_u and P_r

A single plant heterozygous for sugary endosperm and the purple aleurone factor was back-crossed by Dr. EMERSON to a homozygous sugary plant

with red aleurone. There were produced 166 purple starchy and 188 red starchy seeds and 89 purple sugary and 88 red sugary seeds. Both the starchy and sugary seeds were purple and red in approximately equal

TABLE 26

Progeny from the back-cross $T_u\ t_u\ J\ j \times t_u\ t_u\ j\ j$.

PEDIGREE NUMBERS	$J\ T_u$	$J\ t_u$	$j\ T_u$	$j\ t_u$
412	15	24	8	11
413	13	14	10	9
414	11	14	6	3
415	32	31	27	33
416	15	15	6	12
417	55	52	40	39
418	10	12	4	15
419	8	5	2	2
420	9	6	6	1
Totals	168	173	109	125

numbers. Of the 501 seeds produced, 247 had the parental combinations and 254 the new combinations of these factor pairs. This is a deviation of only 3.5 $\pm$ 7.5 from the equality expected for factors that are inherited independently.

Tests involving T_u and S_u with ramosa ear, $R_a\ r_a$

Factors T_u and R_a

Several plants heterozygous for tunicate ear and *ramosa* ear were back-crossed to non-tunicate *ramosa* plants. The progenies from these back-

TABLE 27

Progeny from the back-cross $T_u\ t_u\ R_a\ r_a \times t_u\ t_u\ r_a\ r_a$.

PEDIGREE NUMBERS	$R_a\ T_u$	$R_a\ t_u$	$r_a\ T_u$	$r_a\ t_u$
439	73	95	93	72
441	10	9	7	13
442	20	25	16	10
440	26	22	33	39
Totals	129	151	149	134

crosses are given in table 27. There were produced 280 normal and 283 *ramosa* plants. Of the normal plants 129 were tunicate and 151 non-tunicate, and of the *ramosa* plants 149 were tunicate and 134 non-tunicate. Plants in which both the tunicate and *ramosa* characters are involved have

a much-branched, succulent and wholly sterile ear. This type of sterile ear has been referred to by COLLINS (1917) as the "cauliflower" type of inflorescence. From table 27 it may be seen that 263 plants had the parental combinations and 300 plants had the new combinations of these factor pairs. This is a deviation of 18.5 ± 8.0 from equality. A deviation as large as this would be expected about once in every eight trials, due to the errors of random sampling.

Factors S_u and R_a

A number of back-crosses involving sugary endosperm and *ramosa* plant were made by EMERSON with the results shown in table 28. Starchy

TABLE 28

Progeny from the back-cross $S_u\ s_u\ R_a\ r_a \times s_u\ s_u\ r_a\ r_a$.

PEDIGREE NUMBERS	$S_u\ R_a$	$S_u\ r_a$	$s_u\ R_a$	$s_u\ r_a$
E8024–6 × E8035–10	72	65	42	47
E8014–1 × E8035–14	57	73	44	51
E8024–1 × E8035–20	83	73	53	51
E8014–8 × E8035–14	61	62	60	60
Totals	273	273	199	209

and sugary seeds were produced in approximately equal numbers. The starchy seeds produced normal and *ramosa* plants in equal numbers, there being 273 of each. From the sugary seeds were grown 199 normal and 209 *ramosa* plants, a close approximation to a 1:1 ratio. There were in the total progenies 482 plants with the factorial constitution of the parents and 472 plants with these factors in new combinations. This is a deviation of 5.0 ± 10.4 from the equality expected for factors that are not linked.

These data indicate that the factor pair for *ramosa* ear does not belong to the T_u-S_u linkage group.

Tests involving T_u and S_u with green striping, G_s g_s

Factors T_u and G_s

A number of plants heterozygous for tunicate ear and the chlorophyll pattern called green striping were back-crossed to non-tunicate green-striped plants. Relatively large plantings from these back-crossed ears were made in 1918 but because of a number of unfavorable conditions, including an unusually early killing frost, it was not possible to note the green-striped plants for the tunicate character. The green plants were

noted for the tunicate character with the results given in table 29. There were 197 green plants and 201 that were green striped, a good 1:1 ratio. Of the green plants 104 were tunicate and 93 non-tunicate. This is a deviation of 5.5 ± 4.7 from equality and indicates that the factors are independent.

Tests involving sugary endosperm with the green-striping chlorophyll pattern have not yet been made.

TABLE 29

Progeny from the back-cross $T_u\ t_u\ G_a\ g_a \times t_u\ t_u\ g_a\ g_a$.

PEDIGREE NUMBERS	$G_a\ T_u$	$G_a\ t_u$	$g_a\ T_u + g_a\ t_u$
85	7	11	18
86	18	10	25
87	48	47	101
88	7	3	5
89	24	22	52
Totals	104	93	201

Tests involving T_u and S_u with virescent-white seedling, $V\ v$

Factors T_u and V

A plant heterozygous for virescent-white seedling and recessive for the tunicate character was crossed with a heterozygous tunicate plant that was homozygous dominant for the virescent-white seedling factor pair. This cross may be represented factorially as $t_u\ t_u\ V\ v \times T_u\ t_u\ V\ V$. Tunicate and non-tunicate plants in approximately equal numbers were produced. Half of the tunicate as well as half of the non-tunicate plants should be heterozygous for virescent-white seedling. A number of the tunicate plants of this progeny were self-pollinated. A few seeds from each self-pollinated ear were planted in the greenhouse to determine which of the parent plants were heterozygous for virescent-white seedling. The heterozygous plants were expected to produce green and virescent-white seedlings in a 3:1 ratio. The seedlings from plant 130-7 were found to segregate in this manner. A field-planting from this ear produced 65 green plants and it was found that 46 were tunicate and 19 non-tunicate. These numbers are relatively small but suggest a 3:1 ratio which one would expect if the factor pairs are inherited independently. Theoretically there should have been produced 9 tunicate green: 3 non-tunicate green: 3 tunicate virescent-white: 1 non-tunicate virescent-white plants. Plants homozygous for

virescent-white seedling usually die shortly after germination and only plants of the constitution *V v* and *V V* grow to maturity. Of the green plants that grew to maturity there were expected 3 tunicate: 1 non-tunicate plants in case the factor pair for tunicate ear and virescent-white seedling are independent. The observed numbers approach these expected numbers.

No tests involving sugary endosperm and virescent-white seedling have yet been made.

Tests involving T_u and S_u with white seedling, W w

Factors T_u and *W*

A plant heterozygous for tunicate ear and white seedling was self-pollinated and produced in the F_2 generation 258 mature green plants. Of these 181 were tunicate and 77 non-tunicate. Plants recessive for the white-seedling factor die in the seedling stage and only plants of the constitution *W w* and *W W* grow to maturity. The green plants which survived and matured were expected to be tunicate and non-tunicate in a 3:1 ratio in case the factor pairs are independent. Although the numbers are small they approach this ratio closely enough, deviation 12.5 ± 4.7, to suggest that the factors for tunicate ear and white seedling are not linked.

Tests involving sugary endosperm with white seedling were not made.

Tests involving T_u and S_u with yellow endosperm, Y y

Factors T_u and *Y*

A back-cross involving tunicate ear and yellow endosperm color gave progenies as shown in table 30. These back-crossed ears contained yellow

TABLE 30

Progeny from the back-cross $T_u\ t_u\ Y\ y \times t_u\ t_u\ y\ y$.

PEDIGREE NUMBERS	$Y\ T_u$	$Y\ t_u$	$y\ T_u$	$y\ t_u$
471–472	23	29	20	25
473–474	6	14	10	9
Totals	29	43	30	34

and white seeds in approximately equal numbers. The yellow seeds produced 29 tunicate and 43 non-tunicate plants. The white seeds produced 30 tunicate and 34 non-tunicate plants. The numbers are very small but suggest a 1:1 ratio. Of the total number of plants 63 had the parental

and 73 the new combinations of the factors involved. This is a deviation of 5.0 ± 3.9 from the 1:1 ratio expected for independent inheritance.

It was not determined which of the factors for yellow endosperm is here concerned.

No back-cross tests were made involving sugary endosperm with yellow endosperm but F_2 progenies grown by EMERSON gave no indication of linkage.

Tests involving T_u and S_u with pale-yellow endosperm

Factors T_u and pale-yellow endosperm

A back-cross involving tunicate ear and pale-yellow endosperm color gave a total of 205 plants, 109 having grown from pale-yellow seeds and 96 from white seeds. Both pale-yellow and white seeds produced tunicate and non-tunicate plants in approximately equal numbers. The yellow seeds produced 53 tunicate and 56 non-tunicate plants, while the white seeds produced 50 tunicate and 46 non-tunicate plants. Apparently these factors are inherited independently.

No tests involving sugary endosperm with pale-yellow endosperm color were made.

SUMMARY

The data from this study substantiate the conclusion of previous investigators that ordinary tunicate plants represent a case of imperfect dominance. The homozygous tunicate plants are practically sterile.

The factor pairs for tunicate ear and sugary endosperm tend to be inherited together, with a recombination of the factors occurring in about 30 percent of the cases. This may be explained by assuming that these factors are located in the same chromosome and that the recombinations are the result of crossing over.

A statistical study of the data on the linkage between the factor pairs for tunicate ear and sugary endosperm, and between waxy endosperm and the *C* aleurone factor, indicate that crossing over in corn occurs more frequently in microsporogenesis than in megasporogenesis. It has also been found by other investigators that in *Primula sinensis* crossing over apparently occurs more frequently in microsporogenesis.

A summary of the linkage tests involving the factor pairs for tunicate ear and sugary endosperm with the other groups of linked factors is given in table 31. In every test except one the deviation from a 1:1 ratio between

TABLE 31

Summary of the linkage tests between the T_u-S_u group and other linkage groups.

LINKAGE GROUPS	FACTORS INVOLVED	PARENTAL COMBINATIONS	NEW COMBINATIONS	DEVIATION FROM 1:1 RATIO	DEV. / P. E.Diff.
C–Wx–Sh–I	*C–Tu*	452	450	1.0±10.0	0.1
	C–Su	2212	2190	11.0±22.4	0.5
	Wx–Tu	8	10	1.0±1.4	0.7
	Sh–Tu	8	10	1.0±1.4	0.7
	I–Su	340	310	15.0±8.6	1.8
G–R–L	*G–Tu*	340	323	8.5±8.6	1.0
	R–Tu	322	317	2.5±8.5	0.3
	R–Su	1508	1470	19.0±18.4	1.0
B–Lg–Ts	*B–Tu*	692	713	10.5±12.6	0.8
	B–Su	470	504	17.0±10.4	1.6
	Lg–Tu	839	853	7.0±13.9	0.5
	Lg–Su	1062	1028	17.0±15.4	1.1
P–Ts	*P–Su*	350	356	3.0±9.0	0.3
	P–Tu	276	336	30.0±8.3	3.6
Y–Pl	*Pl–Tu*	172	181	4.5±6.2	0.7
	Pl–Su	561	551	5.0±11.2	0.4
A	*A–Tu*	34	40	3.0±2.9	1.0
	A–Su	157	157	0.0±6.0	0.0

TABLE 32

Summary of the tests between the T_u-S_u group and other factors.

FACTORS INVOLVED	PARENTAL COMBINATIONS	NEW COMBINATIONS	DEVIATION FROM A 1:1 RATIO	DEVIATION / P. E.Diff.
Au–Tu	217	247	15.0±7.3	2.0
Bt–Su	161	161	0.0±6.0	0.0
Cr–Tu	217	203	7.0±6.9	1.0
Cr–Su	335	370	17.5±9.0	2.0
D–Tu	233	242	4.5±7.3	0.6
F–Tu	369	364	2.5±9.1	0.3
Ft–Tu	111	109	1.0±5.0	0.2
J–Tu	293	282	5.5±8.1	0.7
Pr–Tu	142	150	4.0±5.8	0.7
Pr–Su	247	254	3.5±7.5	0.5
Ra–Tu	263	300	18.5±8.0	2.3
Ra–Su	482	472	5.0±10.4	0.5
Gs–Tu	104	93	5.5±8.1	0.7
V–Tu	63	73	5.0±3.9	1.3
Tu–Pale-yellow endosperm	99	106	3.5±4.8	0.7

the parental combinations and new combinations is less than twice the probable error. This indicates that the T_u-S_u group is independent of the other groups that have as yet been established. In the test between T_u and P the deviation is nearly four times the probable error but this wide deviation is doubtless due to the extremely unsatisfactory material from which these data were taken, as has already been mentioned.

Linkage tests have also been made between the T_u-S_u group and other mutant factors whose linkage relations are not yet definitely established. A summary of these tests is given in table 32. The data give no evidence that any of these factors belong to the T_u-S_u linkage group. Unfortunately some of these tests were made with only one member of the T_u-S_u group. Such tests are not conclusive as factors located in the same chromosome may be far enough apart so that crossing over occurs in approximately 50 percent of the cases. This would give the same results as if the factors were in different chromosomes and assorted independently.

LITERATURE CITED

ALTENBURG, EDGAR, 1916 Linkage in *Primula sinensis*. Genetics **1**: 354–366.

BREGGER, T. J., 1918 Linkage in maize: the *C* aleurone factor and waxy endosperm. Amer. Nat. **52**: 57–61.

COLLINS, G. N., 1917 Hybrids of *Zea ramosa* and *Zea tunicata*. Jour. Agric. Res. **9**: 383–395. *Pls. 13–21.*

COLLINS, G. N., AND KEMPTON, J. H., 1912 Gametic coupling as a cause of correlations. Amer. Nat. **46**: 569–590.

1913 Inheritance of waxy endosperm in hybrids with sweet corn. U. S. Dept. Agric. Bur. Plant Ind. Circ. 120. pp. 21–27.

CORRENS, C., 1901 Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenien. Bibliotheca Botanica **53**: 1–161.

EAST, E. M., AND HAYES, H. K., 1911 Inheritance in maize. Connecticut Agric. Exp. Sta. Bull. 167. pp. 1–142.

1915 Further experiments on inheritance in maize. Connecticut Agric. Exp. Sta. Bull. 188. pp. 1–31.

EMERSON, R. A., 1912 The inheritance of the ligule and auricles of corn leaves. Ann. Rep. Agric. Exp. Sta. Univ. Nebraska **25**: 81–88.

1918 A fifth pair of factors, *A a*, for aleurone color in maize and its relation to the *C c* and *R r* pairs. Cornell Univ. Mem. **16**: 231–289.

1920 Pistillate-flowered maize plants. Jour. Heredity **11**: 65–76. *Figs. 9–16.*

1921 The genetic relations of general plant color in maize. In manuscript.

GERNERT, W. B., 1912 A new subspecies of *Zea Mays*, L. Amer. Nat. **46**: 616–622.

GOWEN, J. W., 1919 A biometrical study of crossing over. On the mechanism of crossing over in the third chromosome of *Drosophila melanogaster*. Genetics **4**: 205–250.

HUTCHISON, C. B., 1921 Heritable characters in maize: shrunken endosperm. Jour. Heredity **12**: (In press).

JONES, D. F., AND GALLASTEGUI, C. A., 1919 Some factor relations in maize with reference to linkage. Amer. Nat. **53**: 239–246.

KEMPTON, J. H., 1919 Inheritance of waxy endosperm in maize. U. S. Dept. Agric. Bull. 754. pp. 1–99.

LINDSTROM, E. W., 1917 Linkage in maize: Aleurone and chlorophyll factors. Amer. Nat. 51: 225–237.

1918 Chlorophyll inheritance in maize. Cornell Univ. Mem. 13: 1–68.

MORGAN, T. H., 1919 The physical basis of heredity. 305 pp. Philadelphia: J. B. Lippincott Co.

PEARL, R., AND MINER, J. R., 1914 A table for estimating the probable error significance of statistical constants. Maine Agric. Exp. Sta. Bull. 226. pp. 85–88.

THE GLOBE MUTANT IN THE JIMSON WEED (*DATURA STRAMONIUM*)

ALBERT F. BLAKESLEE

Station for Experimental Evolution, Carnegie Institution of Washington, Cold Spring Harbor, New York

Received December 27, 1920

TABLE OF CONTENTS

INTRODUCTION 241
Description of Globes 242
Inheritance of Globe complex 248
Inbreeding of Globes 251
Occurrence of new Globe mutations 252
Pollen sterility 256
DISCUSSION OF RESULTS 262
SUMMARY 263
LITERATURE CITED 264

INTRODUCTION

The "Globe" was the first mutant discovered in the Jimson Weed, perhaps because of the ease with which it can be distinguished from normal plants of this species. Its depressed-globose capsules thickly set with stout spines suggest chestnut burs in appearance. The closely thatched arrangement of its broad leaves in the adult plant as well as the broad entire leaves of its seedlings renders the Globe one of the easiest mutants in the Jimsons to recognize at any stage of development. It is the only one in fact that we have been able to readily pick out in the seed pan. Since usually it has not been necessary to grow plants beyond an early seedling stage when it is desired to distinguish Globes from normals, it has been possible with this mutant to base conclusions on a larger number of individuals than could readily have been obtained if we had been dealing with the other mutant forms.

All the Globes and other Datura mutants of like type are essentially similar in the manner of transmitting their mutant characters. The inheritance is primarily through the female and but slightly or not at all through the male. They all fail to breed true and throw, when selfed, about three normals to one of the parental mutant type. The pollen does

not transmit the mutant character or transmits it only to a small percentage of the offspring. The Globe and several other mutants of Datura have already been briefly described and figured (BLAKESLEE and AVERY 1919) and the relation outlined between their chromosomal constitution and their genetic behavior (BLAKESLEE, BELLING and FARNHAM 1920). It will be sufficient for the present purpose to state that each of the dozen mutants of the Globe type have undergone a duplication of chromosomes in an individual chromosomal set, so that these mutants produce dimorphic gametes with 12 and 13 chromosomes instead of gametes with uniformly 12 chromosomes characteristic of normals. They are called simple trisomic mutants since in any somatic cell one of the 12 sets is a trisome with 3 homologous chromosomes instead of all the sets being disomes with 2 chromosomes each. The chromosomal condition in these forms has been determined by my colleague, Mr. JOHN BELLING, from studies of mitotic figures in the pollen mother cells. The data in the present paper were secured in the main before the chromosomal irregularities in Datura were discovered and will serve as a basis for later discussions of the significance of the chromosomal difference between mutants and normals.

DESCRIPTION OF GLOBES

Photographs of a capsule and of habits of Globe plants have been already given in an earlier publication (BLAKESLEE and AVERY 1919). In figure 1 is shown a 12-inch seed pan with the seedling offspring from a Globe selfed. The culture had been thinned out once by removal of the larger normal seedlings. Of those that remain the Globes can be readily distinguished by their shorter, broader leaves. Often they can be identified at or before the appearance of the second leaf.

The difference in width of early leaves is susceptible of mathematical expression in the ratio of length to width. The second leaf is most convenient for measurement and has been used as the basis of the tabulations in table 1 A. A considerable number of pedigrees containing both Globes and normals were grown in pots in the greenhouse in the winter of 1916–17. Of the plants measured in any pedigree, an equal number of Globes and normals are represented in the table, chosen according to the numerical order on the pot labels. In the second part of the table are given the measurements for both the leaves of plants in which the first two leaves were approximately equal and borne opposite each other at the same node. From the averages of the table it will be observed that the leaves of Globes are actually only slightly wider than comparable normals though distinctly

shorter. Relatively, however, the leaves of Globe plants are decidedly broader than those of normals from the same pedigree. When the first two leaves are borne opposite at the same node they both average narrower than does the second leaf when the first two leaves are at separate nodes.

17249 3/5/18

FIGURE 1.—Globe and normal seedlings in 12-inch seed-pan. Two of the Globes are labeled with a letter *g*. An earlier thinning had removed a large proportion of normals.

Among such plants, however, the Globes still have broader leaves than the comparable normals. While occasionally a Globe from one pedigree shows a narrower leaf than that of a normal in another pedigree, there is no overlapping of the ratios in any single pedigree in either section of the table. Globe seedlings, however, are not picked out from normals in a

TABLE 1

A. Length and width and ratio length to width of second seedling leaves of Globes and normals.

GLOBES				NORMALS			
Plant number	Length	Width	L ÷ W	Plant number	Length	Width	L ÷ W
16460(1)	56	41	1.37	16460(2)	80	43	1.86
16533(2)	20	12	1.67	16533(6)	70	32	2.18
(3)	46	30	1.53	(7)	67	30	2.23
(4)	53	33	1.61	(8)	65	28	2.32
16534(2)	47	28	1.68	16534(6)	78	39	2.00
(3)	46	27	1.70	(7)	72	34	2.12
(4)	55	37	1.49	(8)	61	28	2.18
16539(1)	52	34	1.53	16539(6)	68	24	2.83
16540(2)	53	36	1.47	16540(8)	78	38	2.05
16549(2)	54	32	1.69	16549(3)	77	37	2.08
16550(1)	80	58	1.38	16550(6)	89	37	2.41
(2)	67	38	1.76	(7)	74	35	2.11
(3)	70	46	1.52	(8)	78	30	2.60
16551(1)	71	41	1.73	16551(2)	75	38	1.97
16686(1)	58	35	1.66	16686(6)	81	42	1.93
(2)	62	42	1.48	(7)	80	40	2.00
(4)	59	35	1.69	(8)	68	34	2.00
16688(1)	66	37	1.78	16688(7)	53	22	2.41
(2)	56	36	1.56	(8)	57	26	2.19
(3)	55	33	1.67	(9)	72	31	2.32
(4)	57	35	1.63	(10)	67	31	2.16
(5)	66	38	1.74	(11)	79	39	2.03
16762(1)	56	43	1.30	16762(4)	83	40	2.08
(2)	68	40	1.70	(5)	78	35	2.23
16763(1)	35	32	1.09	16763(12)	79	41	1.93
(2)	63	38	1.66	(14)	76	34	2.24
16766(1)	72	46	1.57	16766(2)	67	33	2.03
16767(1)	72	52	1.38	16767(6)	65	28	2.32
(2)	58	36	1.61	(7)	89	40	2.23
(3)	59	36	1.64	(8)	80	42	1.90
16768(1)	68	40	1.70	16768(7)	77	31	2.48
(2)	65	38	1.71	(8)	80	38	2.11
(3)	65	38	1.71	(9)	60	30	2.00
16770(2)	60	38	1.58	16770(11)	58	29	2.00
(3)	65	41	1.59	(12)	83	38	2.18
(4)	54	39	1.38	(13)	82	38	2.16
16771(2)	67	45	1.49	16771(6)	91	47	1.94
(3)	67	44	1.52	(7)	83	39	2.13
(4)	64	38	1.68	(8)	64	28	2.29
16773(2)	68	46	1.48	16773(5)	85	44	1.93
(3)	75	52	1.44	(6)	74	38	1.95
(4)	68	43	1.58	(7)	86	41	2.10

TABLE 1 (continued)

GLOBES				NORMALS			
Plant number	Length	Width	L ÷ W	Plant number	Length	Width	L ÷ W
16774(5)	66	43	1.53	16774(11)	57	25	2.28
(6)	68	47	1.45	(12)	89	42	2.12
16775(8)	77	60	1.28	16775(11)	78	44	1.77
(9)	64	44	1.45	(12)	65	32	2.03
(10)	66	44	1.50	(13)	83	40	2.08
16776(1)	68	44	1.55	16776(9)	74	36	2.06
(2)	64	44	1.45	(10)	85	46	1.85
(3)	65	45	1.44	(11)	92	48	1.92
16777(1)	62	48	1.29	16777(6)	80	40	2.00
(2)	58	37	1.57	(7)	64	33	1.94
(3)	62	43	1.44	(8)	81	45	1.80
16778(1)	57	31	1.84	16778(3)	32	35	2.34
16779(1)	66	35	1.89	16779(3)	63	30	2.10
(2)	70	49	1.43	(4)	74	29	2.55
16780(1)	60	44	1.36	16780(6)	84	45	1.87
(2)	44	36	1.22	(7)	71	38	1.87
(3)	65	46	1.41	(8)	86	38	2.26
16781(1)	63	43	1.47	16781(8)	85	38	2.24
(2)	66	46	1.43	(9)	84	42	2.00
(3)	53	33	1.61	(10)	96	43	2.23
16782(1)	60	47	1.28	16782(6)	84	43	1.95
(2)	69	50	1.38	(7)	82	37	2.22
16784(1)	69	50	1.38	16784(6)	98	52	1.88
(3)	67	48	1.40	(7)	94	41	2.29
16786(3)	68	44	1.55	16786(5)	83	44	1.89
16787(3)	64	42	1.52	16787(6)	75	42	1.79
(4)	61	39	1.56	(7)	81	39	2.08
(5)	56	36	1.56	(8)	83	44	1.89
16788(1)	69	42	1.64	16788(4)	86	40	2.15
16789(2)	74	54	1.37	16789(8)	98	53	1.85
(3)	73	53	1.38	(9)	86	41	2.10
(4)	67	48	1.40	(10)	86	43	2.00
16790(1)	47	42	1.12	16790(5)	88	40	2.20
(2)	67	48	1.40	(6)	85	45	1.89
(3)	69	47	1.47	(7)	85	48	1.77
16791(2)	68	47	1.45	16791(8)	78	38	2.05
(3)	63	49	1.29	(10)	81	41	1.98
(4)	67	46	1.46	(11)	85	44	1.93
16792(1)	61	45	1.36	16792(6)	87	40	2.18
(2)	70	50	1.40	(7)	87	38	2.29
16794(1)	71	49	1.45	16794(5)	75	40	1.88
(2)	68	43	1.58	(6)	80	44	1.82
(3)	31	27	1.15	(7)	92	47	1.96
(4)	68	50	1.36	(8)	91	49	1.86

TABLE 1 (continued)

GLOBES				NORMALS			
Plant number	Length	Width	L ÷ W	Plant number	Length	Width	L ÷ W
16795(2)	70	50	1.40	16795(6)	92	46	2.00
(3)	62	43	1.44	(7)	70	39	1.79
16797(2)	62	40	1.55	16797(5)	87	42	2.07
(3)	62	41	1.51	(6)	85	40	2.13
16798(1)	70	37	1.89	16798(5)	97	48	2.02
(2)	73	44	1.66	(6)	99	48	2.06
16819(1)	72	55	1.31	16819(4)	67	31	2.16
(2)	67	49	1.37	(5)	70	35	2.00
(3)	70	51	1.37	(6)	70	40	1.75
16821(1)	62	43	1.44	16821(6)	70	32	2.19
(2)	75	40	1.88	(7)	41	20	2.05
16928(1)	31	21	1.48	16928(2)	63	29	2.17
Totals 98	6105	4081	147.97	98	7663	3724	203.80
Averages...	62.3	41.6	1.50±0.011		78.2	38.0	2.06±0.013

B. Length and width and ratio length to width of the first two seedling leaves when borne at first node of Globes and normals.

16540(1)	38	21	1.81	16540(6)	55	23	2.39
	38	21	1.81		58	23	2.52
16763(3)	55	31	1.77	16763(11)	55	23	2.39
	51	28	1.82		51	20	2.55
16774(1)	64	35	1.83	16774(10)	69	30	2.30
	58	33	1.76		75	32	2.34
16786(1)	53	26	2.04	16786(4)	60	23	2.61
	51	25	2.04		67	25	2.68
16791(1)	57	28	2.04	16791(9)	76	28	2.71
	52	28	1.86		76	28	2.71
16793(21)	58	31	1.87	16793(23)	51	19	2.68
	61	35	1.74		49	19	2.58
Totals 6	636	342	23.39	6	742	293	30.46
Averages...	53.0	28.5	1.86±0.021		61.8	24.4	2.53±0.028

culture by the width relations of their leaves alone. The outline of the blade is more broadly ovate in shape, its surface is more depressed along the veins, the margin is less toothed while the petiole, by its slower growth, causes the leaves to be more closely clustered around the young bud.

The Globe mutant differs from normals apparently in all parts of the plant. It forms a complex of characters readily recognized whether the plants in question have purple or white flowers, many or few nodes, or spiny or smooth capsules. Globes like other mutants of this type are

slower in growth than normals and in competition with normals are liable to be crowded out by the latter. Thus the offspring in mass plantings, obtained by selfing Globes, show few if any Globes and these when present are usually suppressed to but a few inches in height.

TABLE 2

Globes selfed and crossed reciprocally with main-line normals. Plants pollinated in greenhouse, 1916–1917. Records taken in seed-pans in greenhouse, 1917–1918.

GLOBE PARENT	NORMAL PARENT	GLOBE SELFED		GLOBE × NORMAL		NORMAL × GLOBE	
		Globe	Normal	Globe	Normal	Globe	Normal
16686(2)	16400(1)	11	45	4	12	1	8
16688(3)	16615(9)	0	1	25	56	0	73
16762(1)	16400(8)	15	55	16	53	1	8
16763(7)	16615(11)	33	116	7	39	1	41
16763(9)	16400(10)	24	145	28	43	2	21
16774(2)	16400(3)	11	55	28	51	3	81
16775(1)	16679(4)	9	41	69	166	14	158
16776(2)	16400(2)	18	57	21	53	0	85
16776(4)	15703(7)	17	27	4	36	0	17
16776(6)	16679(3)	30	63	22	51	3	78
16776(7)	16400(1)	4	8	20	56	1	20
16780(5)	16856(7)	25	54	11	46	2	68
16533(2)	16615(20)	4	18	23	54	1	73
16534(2)	16400(4)	11	30	31	60	0	82
16768(3)	16636(23)	16	81	23	73	0	51
16784(5)	16896(8)	10	26	19	74	0	83
16773(4)	16896(3)	22	68	1	10	8	82
16777(4)	16925(6)	2	13	13	52	0	53
16550(1)	16450(17)	17	67	14	62	0	48
16550(4)	16450(34)	6	15	11	65	2	72
16767(1)	16896(1)	18	40	26	68	2	88
16688(1)	16720(35)	21	37	3	17	2	73
16776(5)	16720(3)	24	66	17	63	2	77
16789(5)	16720(38)	5	13	25	59	1	71
16768(4)	16566(4)	13	52	8	21	0	78
16793(5)	16411(1)	8	76	4	25	4	94
16793(6)	16720(2)	26	113	27	70	3	76

A variety called Round-leaf Globe differs from the typical Globe in having distinctly broader leaves and a lessened vigor of growth. Since it is a rare form which is occasionally produced by Globe parents and when selfed throws the latter, it has been included in our records with the more typical form. Its exclusion would not materially change the ratios obtained.

INHERITANCE OF GLOBE COMPLEX

Early breeding work with the Globe indicated that the manner of its inheritance was not in accord with any simple Mendelian interpretation. A more extensive series of selfs and crosses was therefore carried out in order to determine more accurately the extent to which the Globe complex could be transmitted. A considerable number of Globe plants growing in the greenhouse in 1916–1917 were selfed and crossed reciprocally with main-line normals which had had no known Globe blood in their ancestry. From among these, due to lack of successful pollination of the pot-grown plants, to failure in germination, or to other causes, only 27 Globes showed a complete series. With the exception of a few cultures grown in the field, all the pedigrees were sown in the greenhouse in 1917–1918 and the plants discarded from the seed pans at an early stage of development. Globe

TABLE 3

Summary of table 2.

ORIGIN OF SEED	SEEDS PLANTED	SEEDLINGS	PERCENT SEEDLINGS	GLOBES	NORMALS	PERCENT GLOBES	RATIO G : N
Globe selfed.....	3015	1782	59.10	400	1382	22.45±0.667	1:3.46
Globe × normal.....	2628	1935	73.63	500	1435	25.84±0.671	1:2.87
Normal × Globe.....	2771	1812	65.39	53	1759	2.92±0.266	1:33.19

Percentage difference between offspring from Globe selfed and from Globe × normal = 3.39 ± 0.945. Diff./E. Diff. = 3.59.

seedlings are recognizable often by the time the first leaf opens and usually before the opening of the third. Only in rare cases has it been necessary to pot up doubtful seedlings for later determination.

In table 2 are presented the detailed results and in table 3 the summary of the experiment. In the latter table are given the number of seeds planted and the percentage of recordable seedlings which they produced. It is obvious that a difference exists between the inheritance through the male and that through the female parent. The egg cells of Globes, whether fertilized by Globe pollen or by pollen from normal plants, transmit the Globe complex to only about 25 percent of the offspring. Globe pollen, when used on normal plants, transmits the character to only about 3 percent of the offspring. This figure, though small, is too large to be accounted for by the occurrence of new Globe mutations, in view of the rarity of Globes from normal parents in comparable material shown in table 4.

If 3 percent represents the average number of Globe pollen grains which transmit the mutant character, we should expect a higher proportion of

Globe offspring when Globe pollen is used than when pollen from normals is used on Globe females. The reverse, however, is actually the case and Globes selfed produce a lower percentage of mutant offspring than Globes pollinated by normals. The difference shown in table 3 is 3.6 times its probable error and is undoubtedly significant. The explanation may possibly be connected with a difference in vitality between seedlings produced by self- and those produced by cross-pollination. The fact is at

TABLE 4

Globes and their normal sibs, selfed and crossed reciprocally. Plants pollinated in greenhouse 1916–1917. Records taken in seed-pans in greenhouse 1917–1918.

GLOBE PARENT	NORMAL PARENT	GLOBE SELFED		GLOBE × NORMAL		NORMAL × GLOBE		NORMAL SELFED	
		Globes	Normals	Globes	Normals	Globes	Normals	Globes	Normals
16550(5)	16550(8)	17	86	31	48	0	31	0	97
16774(1)	16774(12)	29	63	2	11			0	98
16781(2)	16781(10)	36	49					0	101
16790(3)	16790(7)	5	74					0	62
16762(2)	16762(5)			23	44			0	71
16686(5)	16686(6)			2	1	0	9	0	69
16534(3)	16534(6)			21	63	0	41		
16775(4)	16775(13)			10	16				
16819(1)	16819(5)	17	69					0	210
	16551(2)							4	122
	16668(2)							0	158
	16751(1)							0	61
Totals.....		104	341	89	183	0	81	4	1049
Percent Globes.....		23.37±1.35		32.72±1.92		0.00		0.380±0.13	
Ratio, Globes: Normals..		1:3.28		1:2.06				1:262.25	

least suggestive that a lower percentage of recordable seedlings were obtained when Globes were selfed than when they were crossed with normals.

That the difference is in some way associated with out-crossing in contrast to selfing is further suggested by the results of crossing Globes with other Globes. There were three such pedigrees in our 1916–1917 greenhouse cultures and four in our 1918–1919 cultures. These 7 pedigrees gave 84 Globes to 189 normals which is 30.8 percent ± 1.88, or a ratio of 1:2.25. The cross Globe × Globe shows thus a higher proportion of Globes in the offspring than the cross Globe × normal and to about the extent one would expect if the pollen transmits the Globe character to slightly less

than 3 percent of the offspring. The numbers involved in the Globe × Globe cross, however, are not large enough to justify one in placing any dependence upon the ratio which they seem to indicate as characteristic for this type of cross, since the difference between the percentages in the two types of crosses in question divided by the probable error of the difference is only 1.4.

A considerable variation is noticeable in table 2 in the ratio of Globe to normal seedlings produced by the mutant parents. We do not find, however, any general agreement in the results such that some Globes are found to produce consistently higher ratios whether selfed or used as males and females in reciprocal crosses. It is therefore probable that the differences which exist are due to environmental factors rather than that individual Globe parents differ genetically for the Globe complex.

The experiment tabulated in tables 2 and 3 shows the inheritance when Globe parents are selfed and crossed reciprocally with normals which had had no Globes in their ancestry. The question naturally arises as to whether the normals thrown by Globes, and therefore with Globe sibs, are genetically more Globe-like in their breeding behavior than unrelated normals. Table 4 shows a series of pedigrees comparable in time and manner of treatment with those in tables 2 and 3. Only one set (that with the parents 16550(5) and 16550(8)) is complete, but the data are sufficient to indicate that the normal offspring of Globes are true normals so far as their breeding behavior is concerned. The only Globes obtained from selfing the ten normals listed in the table came from a single parent No. 16551(2) and the four Globes in this pedigree most reasonably may be classed as new Globe mutations. The matter will be discussed later under the heading of new mutations, but the experiment under discussion shows that we are warranted, in attempting to compute the percentage of new mutations, in classifying all normal parents together whether or not they have Globe relationships.

In table 5 are summarized all the data available in the different years from 1915 to 1920, in regard to the inheritance of Globes in selfs and crosses. The percentage figures do not differ greatly from those already obtained from the more comparable data of table 3. Globes pollinated by normals are still seen to produce more Globes than Globes selfed, and normals pollinated by Globes produce Globes in only a small proportion of the offspring (1.7 percent). Only one out of the 16 normal sibs of Globes produced any Globes when selfed and the occurrence of these unexpected Globe offspring may be attributed to new mutations rather than to the fact that their parents were descended from Globes.

INBREEDING OF GLOBES

The first Globe mutant was discovered in the fall of 1915 in a pedigree of about 100 plants derived from a cross between white spiny and purple spiny stock from Washington, D. C. Seed from an unguarded capsule gave rise to 100 seedlings in the F_1 generation. The Globe seedlings fell somewhat short of 25 percent of the total offspring. Unfortunately a number of the plants were discarded by mistake before the final records

TABLE 5

Summary of results in different years of selfing Globes and normal sibs of Globes and of crossing Globes with normals and normals with Globes.

YEAR	GLOBE SELFED			GLOBE × NORMAL			NORMAL × GLOBE			NORMAL SELFED		
	Seed parents	Globes	Normals	Seed parents	Globes	Normals	Seed parents	Globes	Normals	Seed parents	Globes	Normals
1915–'16	1	7	37				5	0	256			
1916	13	42	191	1	1	12	8	0	208			
1916–'17	44	362	1621	1	9	15	11	1	428			
1917	7	33	175	3	105	246	1	14	172			
1917–'18	60	955	2721	31	439	1380	32	40	1844	10	4	1050
1918–'19	32	1160	2995	14	309	698	8	2	445			
1919	14	341	1156							2	0	117
1919–'20	61	2433	7003							4	0	905
1920	3	71	175									
Totals.....	235	4403	16075	50	917	2351	65	57	3362	16	4	2072
Percent Globes..	21.50±0.206			28.06±0.530			1.67±0.148			0.19±0.064		
Ratio, Globes: Normals.....	1:3.65			1:2.56			1:58.98			1:517.75		

Percentage difference between offspring from Globes selfed and Globes × normals = 6.56±0.839. Diff./E. Diff. = 7.81.

Difference between normals × Globes and normals selfed = 1.48 ± 0.161. Diff./E. Diff. = 9.19.

were taken, and in consequence exact percentages can not be given for this generation. An attempt was made by inbreeding to increase the proportion of Globe seedlings in the offspring of Globe parents. From pedigrees which showed a high proportion of Globes, individual Globes were chosen for selfing. Globes were also selfed from pedigrees which showed a low percentage of Globes but the line was continued from parents in pedigrees which showed a relatively high proportion of the mutant in question. The attempt to increase the proportion of Globes by inbreed-

ing was not successful. The results of the experiment, which has been carried to the tenth generation, are summarized in table 6. It will be noted that, whereas considerable variation exists in the proportion of Globes in the different generations, still there is no general increase from first to last. A detailed analysis, moreover, shows that it makes no apparent difference in the proportion of its Globe offspring whether a Globe parent comes from a pedigree high in Globes or from one low in this mutant.

TABLE 6

Globe mutant: Inheritance in succeeding generations. Plants in P_1 from a cross; those in F_1 from an unguarded capsule; subsequent generations from selfed parents.

Generations.....	P_1	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8	F_9	F_{10}
Seed parents.	1	1	13	37	43	3	1	3	8	3	19
Total plants.	100±	100	242	1622	2635	364	7	178	660	642	2732
Globes.....	1	<25	42	284	645	104	3	46	134	155	651
Normals.....	99±	>75	200	1338	1990	260	4	132	526	487	2081
Percent Globes..	1.00±	<25	17.36 ±1.64	17.51 ±0.64	24.48 ±0.56	28.57 ±1.60	42.86 ±7.07	25.84 ±2.21	20.30 ±1.06	24.14 ±1.14	23.82 ±0.55
Ratio, Globes: Normals...	1:99±	1:3+	1:4.76	1:4.71	1:3.09	1:2.50	1:1.33	1:2.87	1:3.93	1:3.14	1:3.20

OCCURRENCE OF NEW GLOBE MUTATIONS

Inasmuch as the Globe is one of the most readily recognized of all the Datura mutants and has been sought for in our cultures since its first appearance in 1915, it is possible to give more reliable figures in regard to the frequency of its new appearance than could be done for the mutants discovered later. In tables 7–8 is given the occurrence of Globe plants in offspring from selfed parents of the 19 different main lines. The plants were grown about one foot apart in the rows in the field or in pots in the greenhouse. The various lines have the color, spine and node characters indicated in the table. Those listed as named species were kindly sent by Dr. C. M. WOODWORTH, from Madison, Wisconsin, and have been kept in cultivation under the names supplied by him. It is questionable if any of the lines represented in this table are deserving of specific rank. They seem rather to represent various Mendelian segregates or at best biotypes of a single not very variable species, *D. stramonium*.

In the tables are listed all the Globe mutations that have been observed in pedigrees from normal parents. Pedigrees from selfed parents have been kept separate from those derived from crosses between the main lines and from later segregates from such crosses. All seedlings which were not Globes have been listed as normals although in some cases they

TABLE 8

Main lines and occurrence of new Globe mutations from 1915 to 1920. The first mutation found in 1915 is not included. Double-year figures (1915–1916, etc.) indicate greenhouse cultures, single-year dates

NUMBER	TYPE	ORIGIN	1915–1916		1916				1916–1917				1917				1917–1918			
			Seed parents	Normal	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe
1	P ar M	Washington, D. C.	2	257	21	1046	3	0.286	8	506			5	242						
2	W ar M	Washington, D. C.	2	117	4	262			6	272			2	130						
3	W ar F	Erfurt, Germany	1	207					2	70			1	155						
4	W in F	Erfurt, Germany	4	356	6	390			4	166			1	67						
5	P ar M	Staten Island, N. Y.	2	85	9	291			1	47			1	70						
6	W ar M	Staten Island, N Y.	3	243	19	496			3	285			6	149						
7	W ar M	Bronx, N. Y.			4	649			4	190			1	4						
8	W ar M	Woodbury, N. Y.							2	34			1	37						
9	P ar M	Cold Spring Harbor, N. Y.			1	246	1	0.405	7	212	1	0.469	1	33						
10	P ar M	Charlotte, Va.															1	36		
11	P ar M	Danville, N. C.															1	41		
12	W ar M	Lloyds Neck, N. Y.																		
13	W ar F	J. L. Childs							1	3			1	30						
14	W ar F	Naples, Italy							1	71			1	44						
15	P ar M	*D. stramonium gigantea*															1	2		
16	P ar F	*D. Leichhardtii*															1	3		
17	W in F	*D. laevis*															1	13		
18	P ar M	*D. ferox*															1	15		
19	W ar F	*D. quercifolia*															1	22		
Totals—Main lines inbred			14	1265	64	3380	4	0.118	39	1856	1	0.054	21	961			7	132		
F_1's			7	394	36	1777	1	0.056	70	3394			43	1471	1	0.068				
Back-crosses			4	224	40	1399			4	157			9	291						
Extractives			5	331	86	3000	3	0.099	25	2131	5	0.234	58	2466			10	1050	4	0.380
Totals—Crosses and extractives			9	949	162	6176	4	0.064	100	5682	5	0.090	110	4228	1	0.024	10	1050	4	0.380
Grand totals			23	2214	228	9556	8	0.084	139	7538	6	0.080	131	5189	1	0.019	17	1182	4	0.337

TABLE 8

indicate garden cultures Under "Type," P stands for the Mendelian character purple and W for white, ar for armed capsules and in for inermis, M for many nodes and F for few nodes.

1917-1918				1918				1918-1919				1919		1919-1920		1920				ALL YEARS			
Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Seed parents	Normal	Seed parents	Normal	Globe	Percent Globe	Seed parents	Normal	Globe	Percent Globe
				1	40			1	150	1	0.662	1	72			11	1000	2	0.200	50	3313	6	0.181±0.050
				2	145			1	160			1	111			1	79			19	1292		
				2	72			1	164			1	97			1	89			9	854		
				2	194			1	124			1	91			1	91			20	1479		
				1	42			1	220			1	83			1	95			17	933		
				1	27			1	169			1	6			1	87			35	1462		
				1	14			1	180			1	52			1	97			13	1186		
				1	24			1	176			1	16			1	90			7	377		
				1	31			1	207			1	17			1	98			13	844	2	0.236±0.112
1	36			1	46			1	96			1	125			1	91			5	394		
1	41			1	48			1	129			1	120			2	248			6	595		
																1	92			1	92		
				1	189			1	217			1	98			1	88			6	625		
				1	38			1	252			1	126			1	96			6	627		
1	2			1	30			1	176			1	116			1	84			5	408		
1	3			1	34			1	194			1	54			1	85			5	370		
1	13			1	34			1	298			1	269			1	87			5	701		
1	15			1	23			1	171	1	0.581	1	102			1	89			5	400	1	0.249±0.168
1	22			3	7							2	549			1	75			7	653		
7	132			23	1038			17	3083	2	0.065	19	2104			30	2761	2	0.072	234	16605	9	0.054±0.012
				1	38	1	2.564	2	12											159	7086	3	0.042±0.016
																				57	2064		
10	1050	4	0.380	4	118			8	1855			4	679	10	385	4	338			215	12353	12	0.091±0.018
10	1050	4	0.380	5	156	1	0.637	10	1867			4	679	10	385	4	338			431	21503	15	0.070±0.012
17	1182	4	0.337	28	1194	1	0.084	27	4950	2	0.040	23	2783	10	385	34	3099	2	0.064	665	38108	24	0.063±0.009

include a small percentage of other mutants. In table 7 are given the individual pedigrees in which the Globe mutations occurred. In table 8 their occurrence in the different lines is given for the different years.

Tables 7–8 represent plants which were germinated in the greenhouse and pricked out into three-inch pots where they remained or from which they were later transplanted to the field. In order to obtain mutants without the excessive labor and space needed for large numbers of indi-

TABLE 7

Detailed records of the occurrence of new Globe mutations in pedigrees from 1915 to 1920 The figures under "main lines represented" refer to races in table 8. Under "parent type," P stands for purple and W for white, ar for armed and in for inermis, M for many nodes and F for few nodes. Q indicates a plant affected with the Quercina disease.

YEAR	PEDIGREE NUMBER	PARENT	PARENT TYPE	MAIN LINES REPRESENTED	GLOBES	NORMALS	PERCENT GLOBES
1915		PS7 × WS4	P ar M × W ar M	1 × 2	1	±99	±1 000
1916	1649	15508(1)	P ar M selfed	1	2	44	4 347
	1650	15508(2)	P ar M selfed	1	1	18	5 263
	1657	15509(4)	P ar M selfed	$F_2(1 \times 2)$	1	26	3 704
	16136	15569(12)	W ar M selfed	$F_3(1 \times 2)$	2	42	4 545
	16257	15690(13) × 15567(4)	P ar M Q × W ar M	1 × 2	1	79	1 250
	16363	C.P.	P ar M selfed	9	1	246	0 405
1916–'17	16507	1645(91)	P ar M Q selfed	$F_2(1 \times 2)$	5	1335	0.371
	16925	C.P.	P ar M selfed	9	1	36	2.703
1917	16881	16359(3) × 16169(50)	W ar M × W in F	7 × 4	1	24	4 000
1917–'18	17382	16551(2)	P ar M selfed	$F_5(1 \times 2)$	4	122	3.175
1918	173	16536(3) × 16679(1)	P ar M × W ar M	1 × 2	1	38	2.564
1918–'19	181	17152(2)	P ar M selfed	1	1	150	0.662
	1827	17572(1)	P ar M selfed	18	1	171	0.581
1920	19601	192(1)	P ar M selfed	1	2	97	2.020

viduals, mass plantings were undertaken. Seeds were thickly sown in rows in the garden. In 1917 the seedlings were not cut out and recorded until late in the season when many of them had reached maturity. The evidence from pedigrees from Globe parents where Globes were expected, showed that normal plants with more vigorous growth tend to crowd out mutants which might otherwise appear in the mass plantings. The mass-planting records for this year, therefore, are of little value in indicating the incidence of mutations. In 1919 and 1920 the mass plantings were better handled in that several times during the season the larger seedlings of normal appearance were thinned out to give a better chance of growth to the smaller seedlings and to those which germinated later. It is prob-

able that few if any mutants were discarded in these early thinnings since the majority of the mutants can be recognized in the seedling stage and moreover their relative weakness of growth would prevent their reaching a discardable size until later in the season. Mass-planting records, however, are not comparable with those of garden and greenhouse cultures handled in the usual manner since undoubtedly many more mutants fail to survive when crowded than when given space for individual development. Table 9 shows the records of mass planting of main lines in 1919 and 1920.

TABLE 9

Occurrence of new Globe mutations in mass plantings of different lines in 1919 and 1920.

LINE NUMBER	1919				1920				1919 + 1920			
	Seed parents	Normals	Globes	Percent Globes	Seed parents	Normals	Globes	Percent Globes	Seed parents	Normals	Globes	Percent Globes
1	5	4955	4	0.081	3	6950	3	0.043	8	11905	7	0.059±0.015
2	2	2167			3	7979			5	10146		
3	1	533			1	1646			2	2179		
4	4	1812			1	435			5	2247		
5	1	1333			1	1884			2	3217		
6	1	333			1	735			2	1068		
7	1	585	1	0.171	1	596			2	1181	1	0.085±0.061
8	1	656			1	958			2	1614		
9	1	630			1	876			2	1506		
10	1	717			1	799			2	1516		
11	1	960			1	876			2	1836		
12												
13	1	225			1	4			2	229		
14	1	226			1	34			2	260		
15					1	1933			1	1933		
16	1	637			3	314			4	951		
17					1	41			1	41		
18					1	885			1	885		
19					3	299			3	299		
Total..	22	15769	5	0.032 ±0.009	26	27244	3	0.011 ±0.004	48	43013	8	0.019±0.004

From the data in tables 7–9 it may be concluded that Globe mutations are relatively infrequent. Taking the data as a whole, including both selfs and crosses, they average for potted seedlings around 0.05 percent or 1 in 2000. For mass plantings they average around 0.019 percent or 1 in 5000. It is evident that they are no more likely to occur as a result of crossing than as a result of selfing. They are consistently somewhat

more frequent in the Washington purple armed stock than in the other main lines both in potted seedlings and in mass plantings. The difference seems significant but the cause for this difference is unknown. As will be shown in later publications, the 12–13 chromosome condition is probably brought about by non-disjunction and factors influencing this process are to be sought for as the ultimate cause of the appearance of new mutations of the Globe type.

TABLE 10

Occurrence of new Globe mutations from mutant parents.

PARENT	MUTANT SELFED				MUTANT × NORMAL				NORMAL × MUTANT			
	Seed parents	Normals	Globes	Percent Globes	Seed parents	Normals	Globes	Percent Globes	Seed parents	Normals	Globes	Percent Globes
Poinsettia	11	968	4	0.41	5	389	1	0.26	3	591	1	0.17
Poinsettia var. Wiry	2	189	0		1	15	0		1	225	1	0.44
Cocklebur	20	1859	1	0.05	8	1047	1	0.10	6	1167	0	
Ilex	8	855	0		5	538	1	0.19	4	975	0	
Mutilated	16	871	1	0.11	8	351	0		4	552	2	0.36
Sugar Loaf	8	413	1	0.24	3	367	0		1	197	0	
Rolled	8	705	1	0.14	2	222	4	1.80	1	245	1	0.41
Reduced	6	707	2	0.28	1	127	1	0.78	1	215	0	
Buckling	8	856	1	0.12	1	106	0		1	246	0	
Glossy	7	897	1	0.11	1	143	0		1	253	0	
Microcarpic	18	994	1	0.10	5	178	0		4	353	0	
Spinach[1]	13	625	8	1.26	3	187	4	2.09	2	377	0	
Totals	125	9939	21	0.211 ±0.031	43	3670	12	0.326 ±0.064	29	5396	5	0.093 ±0.028

Percentage difference between offspring from mutant selfed and mutant × normal = 0.115 ± 0.071. Diff./E. Diff. = 1.62.

Percentage difference between offspring from mutant × normal and normal × mutant = 0.233 ± 0.070. Diff./E. Diff. = 3.33.

We have just discussed the occurrence of Globe mutations from normal parents. It will be of interest to consider the occurrence of this mutant from parents belonging to the other mutant types. In table 10 are shown the percentages of new Globes that have occurred from selfing the various mutants and from crossing them reciprocally with normals. The percentages of Globes are evidently higher than from the main-line parents, a condition which may be partially explained by the fact that most of these mutant parents have come from line No. 1, which has given the

[1] In a previous publication (BLAKESLEE and AVERY 1919) the mutant Spinach was provisionally called Tobacco Leaf.

highest percentage of new Globe mutations. It is of interest to note that mutants when used as females in crosses with normals produce more Globe mutations than the same mutants when selfed, and that, when used as males in crosses with normals, the percentage of Globe mutations is reduced to about the average expected from the assemblage of main-line parents. The difference between the cross mutant × normal and normal × mutant is evidently significant statistically; that between mutant selfed and the cross mutant × normal is not statistically significant when considered alone, the difference being only 1.6 times its probable error. A large proportion of the normals used in the test belonged to line No. 4 in which we have never observed a mutation of any kind. We may therefore be actually comparing lines 1 and 4 as well as mutants and normals. A comparison of table 10 with table 3, however, will be instructive and lead us to the conclusion that the egg cell is not only more effective in transmitting the mutant character, once it has arisen, but is also more effective in originating these mutations than is the pollen grain.

POLLEN STERILITY

In studying the condition of pollen it has been our general practice to investigate three flowers from each plant. The pollen is mounted in 10-percent glycerine and somewhat over 330 grains on the average are counted from each anther. The figures from many of the plants, therefore, represent counts of around 3000 grains. There is generally little difficulty in classification. Grains plump and full of protoplasm have been called good while obviously shriveled grains, completely or largely devoid of protoplasm, have been listed as bad in making up the averages. Occasionally flowers have been found in which the pollen is practically all bad due to unknown factors. In these, however, there is not the sharp distinction between good and bad grains seen in other flowers on the plant. Disease and extreme cold are known to bring this condition about and such flowers in consequence have been considered pathological and not included in the averages, although it has not been possible in every case to determine the exact cause of the abnormal appearance of the grains. Environmental factors evidently have some influence upon the pollen counts since the averages from greenhouse plants do not seem to correspond closely to those from plants in the field. It is hoped that it may be possible at a later date to make a more detailed investigation of pollen sterility in the Globe and other Datura mutants. It seems worth while, however, to present the data already obtained with the Globe as a preliminary contribution to such a study.

TABLE 11

Number of bad pollen grains in Globes and in their normal sibs in flowers tested in late summer 1919.

GLOBES							NORMALS						
Plant number	Flower number	Anther	Bad grains	Good grains	Percent bad per flower	Percent bad per plant	Plant number	Flower number	Anther	Bad grains	Good grains	Percent bad per flower	Percent bad per plant
1930(18)	1	A	24	332			1930(13)	1	A	17	327		
		B	26	330					B	16	314		
		C	20	281	6.91				C	14	319	4.09	4.09
	2	A	20	312									
		B	19	329									
		C	24	299	6.28	6.59							
1930(70)	1	A	19	324									
		B	23	299									
		C	20	319	6.17								
	2	A	47	303									
		B	57	278									
		C	52	287	15.23								
	3	A	30	387									
		B	17	273									
		C	40	276	8.51	9.71							
1930(131)	1	A	26	321									
		B	33	284									
		C	30	305	8.89								
	2	A	21	315									
		B	24	308									
		C	26	317	7.02								
	3	A	27	313									
		B	16	309									
		C	25	316	6.75	7.55							
1954(1)	1	A	31	328			1954(2)	1	A	10	354		
		B	39	354					B	12	378		
		C	24	334	8.47	8.47			C	11	265	3.20	3.20
19119(1)	1	A	16	347									
		B	23	273									
		C	22	347	5.93								
	2	A	13	340									
		B	23	318									
		C	19	321	5.32								
	3	A	20	308									
		B	13	310									
		C	13	335	4.60	5.26							

TABLE 11 (continued)

GLOBES							NORMALS						
Plant number	Flower number	Anther	Bad grains	Good grains	Percent bad per flower	Percent bad per plant	Plant number	Flower number	Anther	Bad grains	Good grains	Percent bad per flower	Percent bad per plant
19120(1)	1	A	32	346			19120(7)	1	A	15	303		
		B	28	340					B	7	329		
		C	22	296	7.71				C	18	336	3.98	
	2	A	41	281				2	A	6	368		
		B	45	346					B	9	286		
		C	36	265	12.03				C	8	324	2.29	
	3	A	29	314				3	A	9	343		
		B	15	287					B	9	322		
		C	21	346	6.42	8.72			C	10	322	2.76	3.01
19120(3)	1	A	29	315									
		B	33	366									
		C	31	324	8.47								
	2	A	28	332									
		B	28	287									
		C	35	343	8.64								
	3	A	38	338									
		B	40	287									
		C	24	276	10.17	9.09							
Totals 7..	18	54	1477	17021	143.52	55.39	3	5	15	171	4890	16.32	10.30
Means...			27.35	315.20	7.97	7.91				11.4	326	3.26	3.43
					±0.415	±0.446						±0.210	±0.183

Differences between the percentages of bad pollen per plant for Globes and normals = 4.48 ± 0.48. Diff./E. Diff. = 9.29.

Experience has shown that pollen of normal Daturas is relatively good. In the field of the microscope, there will be only occasionally a shriveled grain. The average amount of bad pollen of 19 plants taken in the late summer of 1919 from several main lines and from sibs of mutants was 2.7 percent. Over 1000 grains were counted for each plant.

In comparison with normals, Globes have a distinctly higher percentage of defective grains. Table 11 gives the counts on 7 Globes and 3 normal sibs of Globes, which were made in the late summer of 1919. They show the actual counts and the differences between the averages of the individual plants and between the individual flowers on these plants. For flowers, the bad pollen ranges from 4.60 percent to 15.23 percent, while for plants the range is from 5.26 percent to 9.71 percent with a mean of 7.9 percent. On the greenhouse plants of 1919–1920 a more extensive series of counts was undertaken. A total of 79 flowers from 44 plants

was investigated with an average of over 1000 grains tested from each flower. The distribution of the percentages grouped by twos is given in table 12. The mean is 6.99 but the range is greater than that of the plants in table 11 due in part at least to the larger number of flowers involved.

An investigation was made of the possible relation between the percentages of bad pollen and the percentages of Globe offspring from selfed plants. In table 13 A are listed plants from the group of table 12 for which both pollen counts and selfed offspring have been obtained. The first column gives the parent number, the second column gives the number of the individual flower from which a portion of the pollen was tested and the remainder used in selfing its own pistil. The third column gives the percentages of bad pollen in the individual flower tested while the remaining three columns give the proportion of Globes and normals which resulted

TABLE 12

Distribution of percentages of bad pollen in 79 flowers of 44 Globe plants. Counts made from plants in greenhouse, 1919–1920.

	PERCENT BAD POLLEN											TOTAL
	0–1.9	2–3.9	4–5.9	6–7.9	8–9.9	10–11.9	12–13.9	14–15.9	16–17.9	18–19.9	20–21.9	
Number of flowers	5	9	21	15	11	11	4	0	1	0	1	79

from the seeds which these flowers produced. It will be noted that plant 19130 (1) has two flowers tested and plant 19145 (1) has three flowers tested.

Five plants from the 1919 garden cultures were similarly tested with the difference that figures for percentages of bad pollen were taken from averages for the individual plants and not for the individual flowers which were pollinated. They are shown in table 13 B.

At first sight there seems little if any relation between the amount of defective pollen and the percentage of Globes in the offspring. If we arrange the percentages of bad pollen of the plants in tables 13 A and 13 B in grades of 2 percent and obtain the average percentages of Globes in the offspring corresponding to these grades, we are able to arrange the data in tables 14 A and 14 B. In the first of these tables there were 20 pedigrees which came from flowers with pollen 1 to 6 percent bad. They gave around 20 percent Globes. There were 15 pedigrees from flowers with more than 6 percent bad pollen and these showed over 26 percent Globes. There seems to be a division above 6 percent bad pollen represented by the double line in the table separating the pedigrees into two groups with high and low Globe tendencies. A similar relation appears in table 14 B which

TABLE 13 A

Arrangement of individual flowers according to the percentages of bad pollen which they showed and records of the Globes and normals obtained from selfed seeds from these flowers. Parents grown in the greenhouse, 1919–1920.

PARENT	FLOWER NUMBER	PERCENT BAD POLLEN	GLOBES	NORMALS	PERCENT GLOBE
19138(2)		21.26	5	14	26.32
19145(19)	2	16.62	51	142	26.42
19138(6)	1	11.75	23	47	32.86
19145(1)	1	11.48	66	156	29.73
19141(4)	1	11.37	30	81	27.03
19139(4)	2	10.36	78	211	26.99
19136(1)	1	10.18	12	42	22.22
19145(2)	1	9.81	56	173	25.23
19133(3)	3	9.31	14	38	26.92
19146(3)	1	9.25	50	163	23.47
19145(1)	3	8.71	14	46	23.33
19130(1)	3	8.44	10	26	27.78
19145(1)	2	7.64	7	14	33.33
19144(1)	1	7.51	12	48	20.00
19142(1)	1	6.57	28	79	26.17
19145(12)	2	5.76	47	152	23.61
19134(2)	3	5.38	62	198	23.85
19133(3)	1	5.00	22	107	17.05
19141(3)	1	4.88	23	69	25.00
19130(2)	1	4.70	45	136	24.86
19145(12)	1	4.47	11	34	20.00
19146(6)	1	4.12	3	41	6.82
19145(1)	1	3.83	2	32	5.88
19145(14)	1	3.78	90	181	33.21
19147(11)	1	3.36	3	56	5.08
19147(8)	1	2.81	64	176	26.66
19130(1)	4	2.69	19	26	23.17
19145(34)	1	2.26	40	177	18.43
19145(4)	1	2.16	30	141	17.54
19145(11)	4	2.06	79	239	24.84
19145(12)	3	1.95	16	48	25.00
19136(1)	2	1.88	68	159	29.96
19147(8)	2	1.86	10	53	15.87
19145(7)	1	1.77	12	57	17.39
19147(2)	1	1.42	27	138	16.36

TABLE 13 B

Similar to table 13 A except that the pollen counts were taken from garden plants in 1919 and refer to the averages for the individual plants and not for individual flowers.

PARENT	NUMBER OF FLOWERS	PERCENT BAD POLLEN	GLOBES	NORMALS	PERCENT GLOBES
1930(70)	3	9.71	42	97	30.22
19120(3)	3	9.09	3	15	16.67
1954(1)	1	8.47	117	196	37.38
1930(131)	3	7.55	48	268	15.19
19119(1)	3	5.26	10	77	11.49

is a similar grouping of the data of table 13 B except for the fact that the dividing line comes above 8 percent bad pollen. The numbers in these two tables combined are too small to warrant one in placing much confidence in the conclusions which they may seem to suggest, viz., that a large percentage of Globes is associated with a relatively high degree of pollen sterility in their parents. Such a conclusion would seem further questionable in view of the wide variation in Globe percentages corresponding to closely similar degrees of pollen sterility shown in detail in tables 13 A and 13 B.

TABLE 14 A

The data of table 13 A with the percentages of bad pollen arranged in grades of two percent and the corresponding percentages of Globes in the offspring.

	PERCENT BAD POLLEN										
	0–1.9	2–3.9	4–5.9	6–7.9	8–9.9	10–11.9	12–13.9	14–15.9	16–17.9	18–19.9	20–21.9
Percent Globes	20.9	19.2	20.2	26.5	25.4	27.8			26.4		26.3
Number of pedigrees	5	8	7	3	5	5			1		1

TABLE 14 B

An arrangement of the data of table 13 B similar to that in table 14 A.

	PERCENT BAD POLLEN										
	0–1.9	2–3.9	4–5.9	6–7.9	8–9.9	10–11.9	12–13.9	14–15.9	16–17.9	18–19.9	20–21.9
Percent Globes			11.5	15.2	28.1						
Number of pedigrees			1	1	3						

DISCUSSION OF RESULTS

The facts presented in the foregoing pages are the empirical results obtained for the most part before chromosomal duplication was known to be the cause of the Globe and other mutations. A brief but somewhat general discussion of the phenomenon of duplication of chromosomes in Datura has already been given elsewhere (BLAKESLEE, BELLING and FARNHAM 1920). It does not seem desirable at the present time to enter into any extended discussion of the subject.

The detailed study of the Globe has shown that a striking difference exists between the transmission of the mutant character through the egg cells and through the pollen grains. Either the male gametes with an extra chromosome in one of the 12 sets are for the most part non-viable and hence only those with the normal quota of chromosomes are available for germination on the stigma or else the pollen tubes of the abnormal grains are unable to reach the ovules in time to take part in fertilization. The relatively high proportion of defective grains speaks for the first hypothesis. Probably both factors play a part in putting the abnormal male gametes out of commission. Pollinations with a limited number of grains may determine the value of the second hypothesis. Both hypotheses assume like chromosomal behavior in formation of eggs and sperms.

No investigation of the condition of ovules has yet been made. The deviation from a 1:1 ratio of normals to Globes in the offspring of Globes leads one to believe that many of the zygotes which are formed with an extra chromosome are incapable of developing into seeds or that of such seeds many fail to give rise to recordable seedlings. The lessened vigor of all simple-trisomic plants in comparison with normal Daturas leads one to expect them to be suppressed at any stage in their struggle for existence.

The occurrence of new Globe mutations is bound up with the cause of chromosomal duplication. Knowing the mechanism to be affected, it may be possible to induce mutations by the application of appropriate stimuli. It seems probable that a duplication in one set renders more likely a duplication in an entirely different set since new Globe mutations are distinctly more frequent from other simple-trisomic mutants than from normals.

The condition of the pollen has received considerable attention in recent years by students of genetics. It has been assumed by some to be a criterion of hybrid ancestry. The fact that pollen sterility is a common phenomenon in various species and mutants of Oenothera has lent support to the belief that hybridity has played a major rôle in their mutability.

The Globe Datura in comparison with normals is characterized by a distinct amount of pollen sterility. Our tabulations of the occurrence of new Globe mutations, however, indicate that mutations are no more likely to arise as an immediate effect of crossing various main lines than as a result of inbreeding these lines for several generations. All of the mutants of Datura with an odd number of chromosomes so far investigated show a considerable amount of bad pollen. The Globe has served as an example but shows fewer defective grains than the others.

Hybridization between forms with different numbers of chromosomes is one method of bringing about chromosomal irregularities and it is probably the irregularities thus induced rather than the mere fact of hybridization which often accounts for defective pollen in hybrids. Gametic lethals brought in through crosses or arising by mutation are factors which in addition to chromosomal aberrations may be expected to have an injurious effect upon the pollen. The work with Datura at least emphasizes the contention that the presence or absence of a considerable amount of pollen sterility is not alone a safe criterion of the pure or hybrid nature of the species in question.

For assistance in collecting and tabulating the data in the present paper, the writer acknowledges his indebtedness to his assistants, Mr. B. T. AVERY, Jr., Mr. P. A. WARREN, Mr. D. S. WELCH, Miss L. A. MINNS, Mr. J. L. CARTLEDGE and Mr. M. E. FARNHAM.

SUMMARY

1. The Globe is one of 12 recurrent mutations found in the Jimson Weed (*Datura stramonium*).

2. It is characterized in distinction from normals by depressed-globose capsules and by broad and only slightly toothed leaves as well as by a lessened vigor of growth.

3. The cause of the peculiarities of this mutant is the presence of a single extra chromosome in a specific one of the 12 chromosomal sets.

4. Such a form is called a simple-trisomic mutant since in its somatic nucleus one of the 12 sets is a trisome with 3 homologous chromosomes instead of all the sets being disomes with two chromosomes each.

5. When selfed, Globes transmit the mutant character to about 22 percent of the offspring.

6. When crossed with a normal as the male parent, Globes transmit the character to about 26 percent of the offspring.

7. When normals are crossed with a Globe as male parent, the character is transmitted to about 2 percent of the offspring.

8. From the above, it is concluded (a) that the mutant complex is transmitted primarily through the egg cells and (b) is transmitted not at all or only to a slight extent through the pollen; (c) that the deviation in the offspring from an equality of Globes and normals is due to the lessened vitality of the mutant forms; (d) that the higher percentage of Globes obtained by crossing Globes with normals over selfing may be due to an increased vigor brought about by the cross.

9. Inbreeding for ten generations has not increased the proportion of Globes in the offspring.

10. New Globe mutations have occurred in various main lines in about 0.05 percent of the offspring which is about 1 out of 2000 individuals.

11. The offspring from crosses between main lines have shown new Globe mutations in about the same proportion as in the main lines themselves.

12. From the other simple-trisomic mutants, new Globe mutations are more frequent than from normals when the mutant is used as the female parent and is pollinated either by its own pollen or by pollen from a normal.

13. When a normal plant is pollinated by a mutant, new Globe mutations are no more frequent in the offspring than they are in the offspring from normals pollinated by normals.

14. From 12 and 13, it is concluded that new Globe mutations are caused by changes in the formation of the egg cells and not at all or but rarely by changes in the pollen.

15. Normal plants show about 2.7 percent of defective pollen grains.

16. Globes show about 8 percent of defective pollen grains.

17. It is concluded that pollen sterility is characteristic of the Globe as of the other simple-trisomic mutants of Datura.

LITERATURE CITED

BLAKESLEE, A. F., and AVERY, B. T., Jr., 1917 Adzuki beans and Jimson Weeds. Jour. Heredity **8:** 125–131, *figs. 10–14.*

BLAKESLEE, A. F., and AVERY, B. T., Jr., 1919 Mutations in the Jimson Weed. Jour. Heredity **10:** 111–120, *figs. 5–15*

BLAKESLEE, A. F., BELLING, JOHN, and FARNHAM, M. E., 1920 Chromosomal duplication and Mendelian phenomena in Datura mutants. Science N. S. **52:** 388–390.

THE EGG RECORDS OF LIMITED PERIODS AS CRITERIA FOR PREDICTING THE EGG PRODUCTION OF THE WHITE LEGHORN FOWL

J. ARTHUR HARRIS, WM. F. KIRKPATRICK, A. F. BLAKESLEE, D. E. WARNER, AND L. E. CARD

Station for Experimental Evolution, Cold Spring Harbor, New York
and
Storrs Agricultural Experiment Station, Storrs, Connecticut[1]

Received February 9, 1921

TABLE OF CONTENTS

INTRODUCTION 265
Notation and theory employed 270
Tests of equations employed 275
Prediction of annual production from the record of one month 275
Prediction of the production of a group of remaining months from the record of any month 281
Prediction of annual production from the sum of two monthly records 289
Prediction of the production of a group of remaining months from the sum of two monthly records 295
Prediction of annual production from the sum of three monthly records 296
Prediction of the production of a subsequent period from the sum of three monthly records 302
Comparison of the two- and three-month periods as bases for the prediction of the egg record of the subsequent months 307
Comparison of the four periods as bases for the prediction of the egg record of the year 308
SUMMARY AND CONCLUSIONS 308
LITERATURE CITED 309

INTRODUCTION

This paper, which is one of a series dealing with various problems of fecundity in the domestic fowl, has for its purpose the treatment of one phase of the problem of the prediction of the egg production of a long period from the recorded performance of a relatively short period of time.

[1] J. ARTHUR HARRIS and A. F. BLAKESLEE, Resident Investigators, STATION FOR EXPERIMENTAL EVOLUTION; WM. F. KIRKPATRICK and D. E. WARNER, Members of Poultry Department of CONNECTICUT AGRICULTURAL COLLEGE and STORRS AGRICULTURAL EXPERIMENT STATION; L. E. CARD, formerly of the Poultry Department, CONNECTICUT AGRICULTURAL COLLEGE.

From the purely scientific side the interrelationship of the egg production of different periods is a problem of great biological interest. From the economic side, two ends which may be either quite distinct or interdependent, are to be attained by the development and application of formulae for the prediction of the egg production of a bird during any period of the pullet year. The first is the determination of the probable future record of an individual bird from her past performance, as a basis for the decision as to whether she shall be kept for egg production or sold for meat. The second is the estimation of the annual record of a bird as a basis of decision as to whether or not she shall be kept until the following season to be used as a breeder.

It will be evident to those who have had to consider the problems with which we have to deal, that economic factors,—particularly the cost of trap-nesting,—and the purpose for which prediction is being made will have great weight in determining the period and the number of periods to be used in the prediction equations. In determining which birds shall be sold to the commission man and which may be fed with reasonable prospects of profitable returns for the remainder of the year, the breeder is not concerned primarily with the record which the bird makes for the year as a whole. Practically he requires to know what returns she will make for the remainder of the period over which she may be retained in the flock. He has already maintained her for n of the 12 months. The question which the poultryman would like to have answered is whether her record during this period has been such that he can afford to feed and house her for the remaining $12 - n$ months. It is evident that to be of the greatest value for this purpose the prediction should be made from periods as early as possible in the life of the bird. In other words, if birds are to be culled out of the flock and sold for their flesh because they are unprofitable as egg producers, this should be done at a time when the maximum saving in cost of maintenance can be coupled as closely as possible with the maximum sale price.

The correlations required for this purpose are, therefore, those between the record of any period which may be selected as a basis for judgment, and the record of later months.

Since in the selection of birds to be held over for breeders the total annual production is presumably the factor to be chiefly taken into consideration it is evident that the correlations to be determined are those between the record of the individual months and of the year as a whole. It would, of course, be better for this purpose if the records of the entire year were known, but as pointed out by CARD (1917, p. 66) many poultry-

men who feel that they cannot trap-nest for the whole year may be able to do so for a period of one, two or three months. Furthermore, another method of determining the record of individual birds for a given period when a knowledge of the maternity of the individual eggs is not necessary has recently been suggested by ALDER and EGBERT (1918).

In selecting the months to be used in the calculation of prediction equations for practical use one should of course be guided by the experience and needs of commercial poultrymen. It has generally been maintained that culling should not be undertaken until the period of summer production. The price of eggs is highest during the winter and early spring months. If birds have been left in the flock during these months in the hope that they will produce some eggs in the period of generally low production and high price, it would be unwise to discard them just at the time when some return will most probably be made for maintenance rations during a preceding period, unless the price of eggs is too low to pay for the cost of the feed during the period of spring production when most of the birds are laying heavily. Possibly this opinion is partly based on the inadequacy of criteria for eliminating the probably less productive birds early in the season.

Furthermore, the physiological laws underlying egg production should, in so far as possible, be taken into account in selecting the periods upon which prediction equations are to be based. Previous students of fecundity in the domestic fowl have been inclined to recognize certain standard periods. For example, the division of the year adopted in the many papers published by PEARL, SURFACE and their collaborators at the MAINE STATION is the following:

Period of winter egg production: November, December, January and February.

Period of spring egg production: March, April and May.

Period of summer egg production: June, July and August.

Period of autumn egg production: September and October.

This is also the division adopted by CARD (1917, p. 67).

These periods will be used in the present paper, and other combinations added so that there may be a wide range of periods from which selection may be made.

While fully recognizing the foregoing principles we have felt it a part of the biologist's task to furnish a comprehensive series of measures of interrelationships of the egg production of various periods from which any desired equation may be selected. It has, therefore, seemed to us best in this publication to base prediction equations upon a large number

of months and combinations of months in order (a) to determine the months which give the best results and (b) to enable those who wish to predict from any group of months.

In the investigations one phase of which is presented in this paper, we have sought among other things:

(1) To determine the best method of predicting the annual egg production of a bird from the known record of any individual month.

(2) To determine the best method of predicting the annual egg production of a bird from the combined records of two or more months.

(3) To determine the best method of predicting the egg record of a bird during a portion of the year from the record of a single antecedent month or a group of antecedent months.

(4) To compare the relative merits of these several methods of prediction among themselves and to determine thereby which of the methods makes possible the most exact prediction as a basis for determining which is likely to be of the greatest practical value.

We fully recognize, and desire to emphasize especially, the fact that the whole problem of the prediction of future egg production cannot be solved in a single investigation. The problem is exceedingly complex and a number of factors are not taken into consideration at all in the present paper. All that has been attempted is to indicate the possibility of an important line of advance and to lay the foundations, in a series of statistical constants, for wider investigations. Some of these are already in progress. In the meantime, the results presented here may prove useful both from the practical standpoint and in facilitating to some extent further and more adequate investigations.

The first definite step in the direction of the use of the egg record of a short recorded period for the prediction of the probable production during a subsequent or a longer period was, as far as we are aware, taken in 1917 when it was shown (HARRIS, BLAKESLEE, WARNER and KIRKPATRICK 1917) that in a heterogeneous series of birds such as are submitted by practical breeders in egg-laying contests, the October egg production is correlated with that of every other month of the year. The whole subject was carried much further in a second memoir (HARRIS, BLAKESLEE and KIRKPATRICK 1917, 1918) in which the correlations between the records of the individual months and the production of the whole year, between the records of the individual months and of the remaining 11 months of the year, and between the production of 5 of the individual months and the production of all the other individual months, were published for two series of birds. In this paper the equations for the prediction of total

annual production from the record of the individual months were given.

The results given in our second paper (HARRIS, BLAKESLEE and KIRKPATRICK 1917, 1918) show clearly that it is possible to predict with a considerable degree of accuracy the annual egg production of a group of birds from their record for a given month. They also indicate that it is possible within limits to predict the egg production of any month, p, from the egg record of any other month, q.

Almost simultaneously CARD (1917) considered the correlation between the records of various periods as a basis for the prediction of annual egg production. Prediction equations were not, however, given.

While the determination of equations for the prediction of the egg production of a subsequent or a more extended period from the actually recorded production of a limited period must rest upon biometric theory, we have deemed it proper in the testing of these equations to proceed in a purely objective manner.

We have determined a series of prediction equations and have used these equations for estimating the egg production of a series of birds, the egg record of which is unknown as far as the development of the equations is concerned. We then determined the difference between the yield predicted by the equations and the actual yield in the case of each individual bird. The average of these deviations, or any other suitable mathematical constant based upon them, furnishes a criterion of the suitability of the equation for purposes of prediction. That equation is best which predicts most exactly the annual egg yield, or the egg production of any shorter period, for a bird of which the record of a limited period is known.

Since the birds entered in the INTERNATIONAL EGG-LAYING CONTEST at Storrs are drawn from a wide geographical area and are furnished by a large number of breeders, and since the conditions in the different years are maintained as nearly constant as possible, it seemed desirable to utilize records from this contest subsequent to those upon which the equations are based in testing the value of the equations. The problem is: How closely can the actual production of a bird entered in the contest in a given year be predicted from equations based on the records of previous years when one or more months' performance of this bird is known from observation? We have, therefore, as already noted, based the test of our series of equations first of all upon the records secured in Connecticut during the contest year 1917 and 1918.

The equations which we publish are based upon 1840 single-comb White Leghorn birds entered in the INTERNATIONAL EGG-LAYING CONTEST for

the years 1911 to 1917. The prediction equations have been tested upon 415 birds whose records were obtained during the year extending from November 1, 1917, to October 31, 1918.

The justification for the course followed is found in the general principle that a theory should not be tested against the observations upon which it is based.

For practical reasons this paper is limited to a test of the accuracy with which the egg record of a series of 415 birds trap-nested at Storrs during 1917–1918 can be predicted by a series of linear equations based on the experience of the six preceding years, 1911–1917, at the same place. It may be urged that conditions at Storrs are not representative of those prevailing in different parts of the country. Recognizing, for the sake of argument at least, the validity of this objection we have been glad to avail ourselves of records taken elsewhere. These are now being used to test the accuracy with which the production of birds in any locality may be predicted by means of equations based primarily upon experience in another place or with another series of birds. The results of these studies will eventually be published.

NOTATION AND THEORY EMPLOYED

We shall find it convenient to have a simple and rigid notation. Let e represent the recorded egg production of a bird in any month, Σ denote a summation of monthly egg records for a given bird, 1, 2, 3, . . . 12 denote the twelve successive months of the pullet year, i.e., the November of the year in which the bird was hatched until and including the following October. Then e_1, e_2, e_3, . . ., e_{12} represent the November, December, January, . . ., October egg record of a bird with an annual record of $E = \sum_{1}^{12} (e)$ eggs. Further, E_n denotes the total number of eggs laid in any month or group of months subsequent to any given month or group of months used as a basis of prediction, i.e.,

$$E_{11} = E - e_1 = \sum_{2}^{12} (e),\ E_{10} = E - e_1 - e_2 = \sum_{3}^{12} (e),\ \ldots,\ E_1 = e_{12}.$$

In the present paper we have used only the linear prediction equations derived from the means, standard deviations and product-moment coefficients of correlation between the periods, or groups of periods, of egg production, i.e., with equations of the type

$$E = \left(\bar{E} - r_{e_p E}\frac{\sigma_E}{\sigma_{e_p}}\bar{e}_p\right) - r_{e_p E}\frac{\sigma_E}{\sigma_{e_p}}e_p$$

where E represents the annual egg production or the production of any period of months, and e_p denotes the production of any period used as a basis for prediction.

The reader may quite legitimately suggest that in certain cases better prediction might have been secured by the use of regression curves of a higher order. This may be true. Our plan has been to test not merely the linear equations but others as well. Considerable progress has been made toward this end. Comprehensive tests will, we hope, eventually be published. Since, however, a relatively high degree of accuracy of prediction may be attained in most cases by the use of the linear equation, it does not seem proper to withhold useful results until it is possible to determine whether additional refinement can be attained.

The essential characteristics of equations for the prediction of egg yield are two:

1. That the errors of prediction be distributed about the true numbers in such a manner that estimations will not in the long run be either too high or too low.

2. That the magnitude of the deviations of the predicted from the observed egg productions be as small as possible.

Thus in testing formulae by determining how efficiently they predict the production of birds whose record is actually known, we shall consider that formula the best which (a) shows the least error in the direction of consistently too high or too low prediction, and (b) gives the lowest deviation of the predicted from the observed record.

To test the first of these essentials we have merely to determine the average deviation with regard to sign of the predicted from the actually measured egg production. This is given by

$$\frac{\Sigma\,(E'_p - E_p)}{N}$$

where E_p is the actual egg production of a bird, E'_p the theoretical egg record of an individual bird for a period p, and N the number of birds considered. Here a negative sign indicates that the equation has predicted records which are on the average too low, whereas a positive sign indicates that it has predicted records which are on the average too high.

But, as noted above, a formula must do more than fail to consistently overestimate or underestimate. It must give predicted values which show the lowest possible deviation from those determined by trap-nesting. We have, therefore, to consider the test which shall be applied to deter-

mine which formula gives the lowest deviation. Two methods may be suggested.

First, the deviations may be summed without regard to sign and divided by their number. This gives an average deviation without regard to sign of the predicted from the recorded production for any flock and period under consideration.

The disadvantages of this method are two: (a) It ignores mathematical convention with regard to signs. (b) It gives large and small deviations a weight proportional to their actual magnitudes. Thus 50 deviations of 3 eggs each and 50 deviations of 5 eggs each would give an average deviation of 4 eggs, while 50 deviations of 1 egg each, 25 deviations of 6 eggs each and 25 deviations of 8 eggs each would also give a general average deviation of 4 eggs. But since one of the ideals to be attained in the selection of a formula would seem to be to obtain one which will avoid the grosser errors it seems proper to weight the larger deviations. This can be most logically done by squaring. Then

$$\left\{\frac{\Sigma\,(E'_p - E_p)^2}{N}\right\}^{\frac{1}{2}}$$

gives a square root of mean square deviation, or a "root mean square deviation." This is probably the best available measure of the deviation of prediction from observation.

For completeness we shall employ all three methods in the tests of equations used in this paper.

The method of taking the difference has been so chosen that a positive sign, indicating larger error of estimating, shows an inferiority in the equation.

Two of the criteria are values without sign. In the case of the average deviation with regard to sign the criteria may be either positive or negative. In comparing two different methods of prediction we have considered that the *magnitude* of the error and not the *sign* is the critical point. In such comparisons, therefore, all of the criteria have been considered as alike in sign. Cases may possibly arise in which it is desirable to consider the question of over prediction or under prediction by two formulae which may be under consideration. If so our tables of criteria and not the differences as published should be consulted by the reader.

The characteristic equation given above is strictly valid only when applied to the population from which it is deduced. Its extension without modification to another population is justified only if the physical constants

TABLE 1

Comparison of constants for series of birds on which equations were based (1911 to 1917) and series on which they were tested (1917–1918).

	MEAN					STANDARD DEVIATION				
	1911 to 1917	1917 to 1918	Difference	$\frac{\text{Diff.}}{E_{\text{Diff.}}}$	Percentage difference	1911 to 1917	1917 to 1918	Difference	$\frac{\text{Diff.}}{E_{\text{Diff.}}}$	Percentage difference
November	5.20±0.09	5.78±0.20	+0.58±0.21	2.76	11.11	6.00±0.06	6.34±0.14	+0.34±0.15	2.26	5.66
December	6.58±0.11	6.21±0.22	−0.37±0.24	1.54	5.62	7.10±0.07	6.80±0.15	−0.30±0.16	1.87	4.22
January	6.07±0.10	6.63±0.19	+0.56±0.21	2.66	9.22	6.63±0.07	5.83±0.13	−0.80±0.14	5.71	12.06
February	10.10±0.09	9.93±0.19	−0.17±0.21	0.80	1.68	5.91±0.06	5.94±0.13	+0.03±0.14	0.21	0.50
March	17.45±0.08	16.96±0.18	−0.49±0.19	2.58	2.80	5.31±0.05	5.52±0.13	+0.21±0.13	1.62	3.95
April	18.85±0.07	17.48±0.18	−1.37±0.19	7.21	7.26	4.67±0.05	5.44±0.12	+0.77±0.13	5.92	16.48
May	20.55±0.08	21.84±0.16	+1.29±0.17	7.58	6.27	5.24±0.05	5.06±0.11	−0.18±0.12	1.50	3.43
June	20.41±0.09	19.18±0.20	−1.23±0.21	5.85	6.02	5.84±0.06	6.13±0.14	+0.29±0.15	1.93	4.96
July	19.28±0.10	17.96±0.24	−1.32±0.26	5.07	6.84	6.43±0.07	7.43±0.17	+1.00±0.18	5.55	15.55
August	17.10±0.11	16.71±0.26	−0.39±0.28	1.39	2.28	7.30±0.08	7.96±0.18	+0.66±0.19	3.47	9.04
September	11.78±0.13	12.98±0.26	+1.20±0.29	4.13	10.18	8.36±0.09	7.93±0.18	−0.43±0.20	2.15	5.14
October	4.92±0.10	5.87±0.23	+0.95±0.25	3.80	19.30	6.63±0.07	7.07±0.16	+0.44±0.17	2.58	6.63
Annual	158.36±0.68	157.59±1.41	−0.77±1.56	0.49	0.48	43.34±0.48	42.63±0.99	−0.71±1.10	0.64	1.63

and the correlations of the variables in the two populations are essentially identical.

Because of the uniformity of care and the wide origin of the birds exhibited each year at the INTERNATIONAL EGG-LAYING CONTEST at Storrs the average productions do not differ widely in the different years. Thus the monthly and annual averages and standard deviations for the 1840 birds upon which the equations were based and the 415 birds upon which they were tested appear in table 1.[2]

While certain of the differences are significant in comparison with their probable errors it is quite clear that the averages for the two periods are in fair agreement.

Bird 997, Pen 100

	1	2	3	4	5	6	7	8
N		143.1	−17.9	320.41				
D		137.2	−23.8	566.44	161	143.1	−17.9	320.41
J	3	148.1	−12.9	166.41	161	134.4	−26.6	707.56
F	13	169.7	+8.7	75.69	158	135.6	−22.4	501.76
M	24	189.1	+28.1	789.61	145	136.2	−8.8	77.44
A	21	169.2	+8.2	67.24	121	129.2	+8.2	67.24
M	29	199.6	+38.6	1489.96	100	99.4	−0.6	0.36
J	25	180.4	+19.4	376.36	71	92.3	+21.3	453.69
J	27	193.2	+32.2	1036.84	46	61.8	+15.8	249.64
A	13	142.0	−19.0	361.00	19	44.9	+25.9	670.81
S		118.5	−42.5	1806.25	6	12.8	+6.8	46.24
O	6	162.0	+1.0	1.00	6	−0.7	−6.7	44.89
Year	161							

The method followed in the calculations may be illustrated by one of the calculation blanks for the individual bird—No. 997, pen 100. The first column shows the production for the month indicated by the letters on the stub. This serves as the basis of prediction. The second column shows the predicted number of eggs for the year, the third shows the deviation of this predicted number from the annual total of 161 eggs. The fourth column gives the squares of these deviations of prediction from observation. The fifth column shows the number of eggs in the remaining months of the year.[3] The sixth column shows the number of eggs predicted

[2] The percentage differences have been calculated by using the monthly averages for 1911 to 1917 as a base.

[3] The yields for the remaining months (columns 5 to 8) are dropped one space so as to coincide with the first month of the period. For example, bird 997 laid 161 eggs in the period from December to October; 161 in the period from January to October; 158 in the period from February to October, and so on.

for the remaining months. The seventh shows the deviations and the eighth the squares of the deviations of these predicted values from the actual record for the remaining months.

Calculation blanks for each individual bird were made on this principle for each of the equations used. The labor of testing the equation has, therefore, been very heavy, involving the calculation of 29,465 predicted values and the summations of the errors and squares of errors of the deviations of these predicted records from their true value.

The excessive arithmetical routine has been ably handled by Miss EDNA M. PECKHAM, Miss IDA M. PECKHAM, Miss RUTH T. CRAWSON, and Miss KATHLEEN GAVIN of the Biometric Laboratory of the STATION FOR EXPERIMENTAL EVOLUTION. We are indebted to Miss EDNA K. LOCKWOOD for the diagrams, as well as for much assistance in the computations.

TESTS OF EQUATIONS EMPLOYED

Prediction of annual production from the record of one month

Consider first of all the results of the attempts to predict the annual egg production of 415 White Leghorn birds observed at Storrs in 1917–1918 from the records of a single month's production. The equations based on the 1911 to 1917 experience are as follows:

Month from which prediction is made	*Prediction equation*
November	$E = +143.186 + 2.914\ e_1$
December	$E = +137.293 + 3.200\ e_2$
January	$E = +138.271 + 3.308\ e_3$
February	$E = +118.689 + 3.926\ e_4$
March	$E = +76.160 + 4.708\ e_5$
April	$E = +62.688 + 5.074\ e_6$
May	$E = +58.009 + 4.883\ e_7$
June	$E = +59.977 + 4.818\ e_8$
July	$E = +71.137 + 4.523\ e_9$
August	$E = +90.391 + 3.974\ e_{10}$
September	$E = +118.509 + 3.381\ e_{11}$
October	$E = +141.470 + 3.429\ e_{12}$

These are in good general agreement with the equations for two of the years, 1913–1914 and 1914–1915, published in a former paper (HARRIS, BLAKESLEE and KIRKPATRICK 1918, page 33, table 5). The graphical tests for linearity of regression (*loc. cit.*, diagrams 2–5, p. 34–39) for these two years, indicate a fairly close approximation to linearity throughout the greater part of the range of variation of monthly egg production. A critical test of linearity presents some difficulties because of the concen-

tration of the bulk of the birds into a few of the classes, with the result that a rather large number of classes contain only a few birds each. A closer study of the fit of the regression line may, therefore, be deferred until more data are in hand.

The results of the tests of accuracy of prediction in the 415 White Leghorn birds of the 1917–1918 contest are given in tables 2 to 4. Since later

TABLE 2

Average deviation with regard to sign of predicted annual egg record from actual record. Prediction of annual production from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	+2.39	1.52	Nov. + Dec.	+1.16	0.74	+1.23	+0.78
	December	−0.49	0.31	Nov. + Dec.	+1.16	0.74	−0.67	−0.43
	December	−0.49	0.31	Dec. + Jan.	+1.15	0.73	−0.66	−0.42
	January	+2.58	1.64	Dec. + Jan.	+1.15	0.73	+1.43	+0.91
	January	+2.58	1.64	Jan. + Feb.	+1.75	1.11	+0.83	+0.53
	February	+0.06	0.04	Jan. + Feb.	+1.75	1.11	−1.69	−1.07
	February	+0.06	0.04	Feb. + Mar.	−1.22	0.77	−1.16	−0.73
	March	−1.63	1.03	Feb. + Mar.	−1.22	0.77	+0.41	+0.26
	March	−1.63	1.03	Mar. + Apr.	−4.94	3.13	−3.31	−2.10
	April	−6.23	3.95	Mar. + Apr.	−4.94	3.13	+1.29	+0.82
	April	−6.23	3.95	Apr. + May	+0.48	0.30	+5.75	+3.65
	May	+7.02	4.45	Apr. + May	+0.48	0.30	+6.54	+4.15
	May	+7.02	4.45	May + June	+0.82	0.52	+6.20	+3.93
	June	−5.21	3.31	May + June	+0.82	0.52	+4.39	+2.79
	June	−5.21	3.31	June + July	−6.60	4.19	−1.39	−0.88
	July	−5.27	3.34	June + July	−6.60	4.19	−1.33	−0.85
	July	−5.27	3.34	July + Aug.	−3.81	2.42	+1.46	+0.92
	August	−0.82	0.52	July + Aug.	−3.81	2.42	−2.99	−1.90
	August	−0.82	0.52	Aug. + Sept.	+2.60	1.65	−1.78	−1.13
	September	+4.78	3.03	Aug. + Sept.	+2.60	1.65	+2.18	+1.38
	September	+4.78	3.03	Sept. + Oct.	+5.34	3.39	−0.56	−0.36
	October	+3.95	2.51	Sept. + Oct.	+5.34	3.39	−1.39	−0.88

we shall have to compare the results for prediction from one month's performance with that from two- and from three-months record it has been desirable to give the results side by side in the same table. The reader need not, therefore, concern himself with the values for prediction from two-months production until later. Since the errors of prediction of the annual record from each individual month must be compared with the results for prediction from the combined production of two months, the constants for the single months have been given in duplicate.

The average errors with regard to sign are generally low, that for prediction from November and from January production gives on the average 2.4 eggs too many for the year. For December, February, March and August the prediction is in error by less than 2 eggs. The values predicted from April, May, June, July, September and October records are about 4 to 7 eggs in error.

TABLE 3

Average deviation without regard to sign of predicted annual egg record from actual record. Prediction of annual production from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	29.59	18.78	Nov. + Dec.	28.09	17.82	+1.50	+0.96
	December	29.26	18.57	Nov. + Dec.	28.09	17.82	+1.17	+0.75
	December	29.26	18.57	Dec. + Jan.	27.23	17.28	+2.03	+1.29
	January	30.09	19.09	Dec. + Jan.	27.23	17.28	+2.86	+1.81
	January	30.09	19.09	Jan. + Feb.	27.35	17.35	+2.74	+1.74
	February	27.28	17.31	Jan. + Feb.	27.35	17.35	−0.07	−0.04
	February	27.28	17.31	Feb. + Mar.	25.04	15.89	+2.24	+1.42
	March	27.95	17.73	Feb. + Mar.	25.04	15.89	+2.91	+1.84
	March	27.95	17.73	Mar. + Apr.	26.74	16.97	+1.21	+0.76
	April	28.72	18.22	Mar. + Apr.	26.74	16.97	+1.98	+1.25
	April	28.72	18.22	Apr. + May	26.68	16.93	+2.04	+1.29
	May	28.62	18.16	Apr. + May	26.68	16.93	+1.94	+1.23
	May	28.62	18.16	May + June	25.99	16.49	+2.63	+1.67
	June	29.03	18.42	May + June	25.99	16.49	+3.04	+1.93
	June	29.03	18.42	June + July	26.17	16.61	+2.86	+1.81
	July	28.35	17.99	June + July	26.17	16.61	+2.18	+1.38
	July	28.35	17.99	July + Aug.	24.88	15.79	+3.47	+2.20
	August	26.87	17.05	July + Aug.	24.88	15.79	+1.99	+1.26
	August	26.87	17.05	Aug. + Sept.	23.18	14.71	+3.69	+2.34
	September	24.78	15.72	Aug. + Sept.	23.18	14.71	+1.60	+1.01
	September	24.78	15.72	Sept. + Oct.	23.93	15.18	+0.85	+0.54
	October	27.37	17.37	Sept. + Oct.	23.93	15.18	+3.44	+2.19

The average deviations without regard to sign are of course much larger since they constitute a measure of the error of prediction of the records of individual birds. They range from 24.8 to 30.1 eggs. The significance of errors of this magnitude will be more clearly brought out later.

The square root of mean square deviation also shows considerable regularity from month to month. These measures are naturally considerably larger than the average deviation without regard to sign. They range from 32.9 to 38.8 eggs.

It is clear that the annual egg production of birds similar in origin to the series upon which the prediction equations were based and maintained under similar conditions may be predicted with a relatively high degree of accuracy providing their record for any month is definitely known.

The accuracy with which prediction may be made will be clear if the errors of prediction are expressed in terms of the actual average annual production of the group of birds upon which the test is made.

TABLE 4

Square root of mean square deviation of predicted annual egg record from actual record. Prediction of annual production from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	38.65	24.52	Nov. + Dec.	36.46	23.13	+2.19	+1.39
	December	37.61	23.86	Nov. + Dec.	36.46	23.13	+1.15	+0.73
	December	37.61	23.86	Dec. + Jan.	35.50	22.53	+2.11	+1.33
	January	38.77	24.60	Dec. + Jan.	35.50	22.53	+3.27	+2.07
	January	38.77	24.60	Jan. + Feb.	34.32	21.78	+4.45	+2.82
	February	34.70	22.02	Jan. + Feb.	34.32	21.78	+0.38	+0.24
	February	34.70	22.02	Feb. + Mar.	31.32	19.87	+3.38	+2.15
	March	34.28	21.75	Feb. + Mar.	31.32	19.87	+2.96	+1.88
	March	34.28	21.75	Mar. + Apr.	32.89	20.87	+1.39	+0.88
	April	35.31	22.40	Mar. + Apr.	32.89	20.87	+2.42	+1.53
	April	35.31	22.40	Apr. + May	32.76	20.79	+2.55	+1.61
	May	35.89	22.77	Apr. + May	32.76	20.79	+3.13	+1.98
	May	35.89	22.77	May + June	32.53	20.64	+3.36	+2.13
	June	36.53	23.18	May + June	32.53	20.64	+4.00	+2.54
	June	36.53	23.18	June + July	33.00	20.94	+3.53	+2.24
	July	35.89	22.77	June + July	33.00	20.94	+2.89	+1.83
	July	35.89	22.77	July + Aug.	31.83	20.20	+4.06	+2.57
	August	34.34	21.79	July + Aug.	31.83	20.20	+2.51	+1.59
	August	34.34	21.79	Aug. + Sept.	30.39	19.28	+3.95	+2.51
	September	32.94	20.90	Aug. + Sept.	30.39	19.28	+2.55	+1.62
	September	32.94	20.90	Sept. + Oct.	32.74	20.77	+0.20	+0.13
	October	36.47	23.14	Sept. + Oct.	32.74	20.77	+3.73	+2.37

Remembering that the average annual production of the 415 test birds is 157.573 eggs, we use this as a base to determine the percentage errors for the equations for each month. These are given in columns with the caption "percentage deviation" in the tables.

We note that in predicting from December, February and August record the average error with regard to sign *is less than one percent of the average annual yield of the flock.* In predicting from November, January

and March the error lies between one and two percent. When April, May, June, July, September and October records are used as a basis the average errors of prediction are about 2.50 to 4.50 percent of the average annual yield.

The average deviations without regard to sign are less than 20 percent of the annual production. The values for the individual months range from 15.7 for September to 19.1 for January.

The square root of mean square deviations are less than 25 percent of the average annual production. The individual values range from 20.9 for September to 24.6 for January.

These two latter tests may at first seem to indicate very unsatisfactory prediction. Such, however, is not the case. These give the average errors *either above or below the true record made in the prediction of the results for an individual bird*. The thing which is required in practice is generally *the prediction for a group of birds of a particular class*. In a flock of 415 birds this has been shown above to be possible *with an error of less than 5 percent of the actual production for any month of the year and less than one percent for a number of the months*.

The closeness of prediction may be made clear by a set of diagrams.

In these the estimated production is shown by the straight line. The actual average production for the year or for the group of remaining months for which prediction is made is shown by solid dots for each group of birds as classified by monthly record. The shaded areas are determined as follows. The birds were first grouped into classes of five-eggs range with respect to number of eggs laid during the period of time used as a basis of prediction. The birds of these classes of five-eggs range were further subdivided into those in which actual egg production was greater than the predicted and those in which the actual number was less than the predicted number.[4] The average error of prediction was determined for each of these groups, and these averages represent the upper and the lower limits of the shaded areas. The upper limit represents, therefore, the average deviation (for the period for which prediction is made) of all birds which make a higher record than that predicted for their class. The lower limit

[4] A range of five eggs was used in order to obtain a number of birds sufficiently large to reduce somewhat the irregularities due to the errors of random sampling. The errors of prediction were in each case determined for classes of unit range. Grouping is used for graphic representation merely. The average deviations represented by the limits of the shaded zone are to be thought of as measured from a line perpendicular to the ordinates and intersecting the prediction line on the mid-ordinate of the 5-egg class.

of the shaded area marks the average deviation for all birds which show an egg record lower than that predicted.

The graphs representing the prediction of annual production from the individual-months production appear in diagram 1 for the first six months of the year and in diagram 2 for the last half of the year.

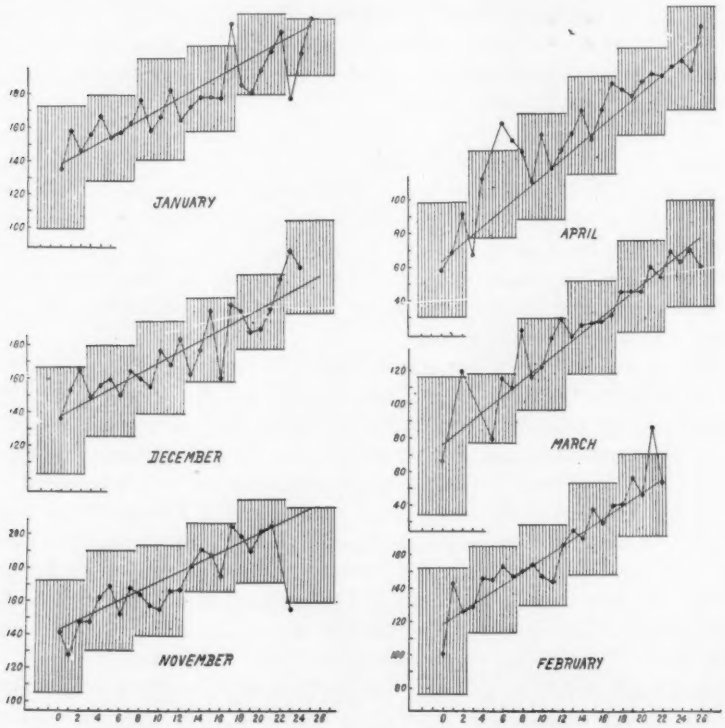

DIAGRAM 1.—Tests of prediction of annual production from single-month records. Month of November to April. For explanation see text.

Notwithstanding the irregularities which are inevitable in graphs based on such a highly variable character as annual egg production in a flock of only 415 birds, the most critical reader must admit that the prediction is excellent.

Prediction of the production of a group of remaining months from the record of any month

As noted above (pages 266–268) the worker may desire to predict either the total egg production for the year or the egg production for a group of subsequent months of the year.

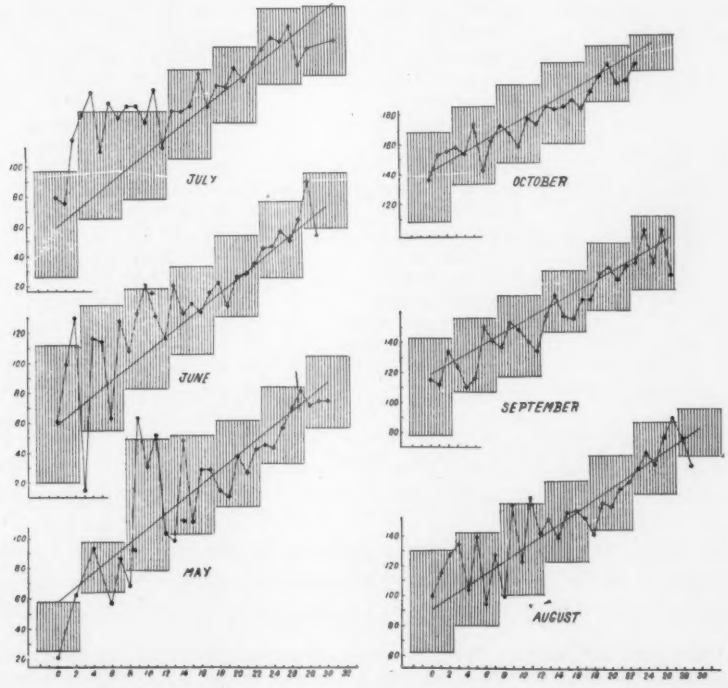

DIAGRAM 2.—Tests of prediction of annual production from single-month records. Tests for May to October.

In general the requirement will probably be the prediction of the total egg production of the remaining months of the year. Since, however, it is necessary to deal with other groups later, the errors of prediction of (a) the total egg production of the months of the year subsequent to the *p*th

month, where p is the base of prediction and of (b) the months of the year subsequent to the $(p + 1)$th month will be considered in this place.[5]

The equations required are as follows:

Month from which prediction is made	*Period for which prediction is made*	*Prediction equation*
November	December to October	$E_{11} = +143.186 + 1.914\ e_1$
November	January to October	$E_{10} = +139.262 + 1.403\ e_1$
December	January to October	$E_{10} = +134.491 + 1.835\ e_2$
December	February to October	$E_9 = +131.461 + 1.373\ e_2$
January	February to October	$E_9 = +130.997 + 1.564\ e_3$
January	March to October	$E_8 = +123.011 + 1.215\ e_3$
February	March to October	$E_8 = +109.824 + 2.035\ e_4$
February	April to October	$E_7 = +96.619 + 1.614\ e_4$
March	April to October	$E_7 = +69.966 + 2.471\ e_5$
March	May to October	$E_6 = +60.338 + 1.932\ e_5$
April	May to October	$E_6 = +46.490 + 2.523\ e_6$
April	June to October	$E_5 = +39.849 + 1.786\ e_6$
May	June to October	$E_5 = +27.639 + 2.233\ e_7$
May	July to October	$E_4 = +20.623 + 1.581\ e_7$
June	July to October	$E_4 = +13.895 + 1.920\ e_8$
June	August to October	$E_3 = +8.740 + 1.228\ e_8$
July	August to October	$E_3 = +6.049 + 1.440\ e_9$
July	September to October	$E_2 = +2.323 + 0.746\ e_9$
August	September to October	$E_2 = +0.724 + 0.935\ e_{10}$
August	October	$E_1 = +0.407 + 0.264\ e_{10}$
September	October	$E_1 = -0.726 + 0.480\ e_{11}$

The test of accuracy of prediction of these equations when applied to the 415 White Leghorns of 1917–1918 is given in comparison with the results for the prediction from two-months production (to be discussed later) in tables 5 to 7.

Limiting our attention for the moment to the errors of predicting the production of the months of the year remaining after any given month used as a basis of prediction, we note that in general the average deviations

[5] In the comparison between the egg production of a period of two months and the egg production of a single month as a basis of prediction, it is necessary to base critical comparisons upon the results of predictions of the records of periods subsequent to the two months under consideration. Concretely, if we are to compare November-plus-December record with November record and with December record as bases for the prediction of the annual production, the two-month period will contribute more to the annual record than either of the two months individually considered. Neither will contribute to the January-to-October production. We must, therefore, in testing prediction equations, base the test upon the results secured in predicting January-to-October egg record.

For this purpose we must have equations which show the relation between the egg record of the individual months and the egg record of groups of remaining months. For example, we require for November the January-to-October production; for December, the February-to-October production; for January, the March-to-October production and so on. For convenience merely the equations are given here in comparison with the other one-month equations.

TABLE 5

Average deviation with regard to sign of egg record for a period of months from actual record. Prediction from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Dec. to Oct.....	November	+2.39	1.57	—	—	—	—	—
Jan. to Oct.....	November	+1.73	1.19	Nov. + Dec.	+1.16	0.80	+0.57	+0.39
Jan. to Oct.....	December	+0.24	0.16	Nov. + Dec.	+1.16	0.80	−0.92	−0.64
Feb. to Oct.....	December	+0.98	0.71	Dec. + Jan.	+1.69	1.22	−0.71	−0.51
Feb. to Oct.....	January	+2.37	1.71	Dec. + Jan.	+1.69	1.22	+0.68	+0.49
Mar. to Oct.....	January	+2.02	1.57	Jan. + Feb.	+1.45	1.12	+0.57	+0.45
Mar. to Oct.....	February	+0.09	0.77	Jan. + Feb.	+1.45	1.12	−1.36	−0.35
Apr. to Oct.....	February	+0.56	0.50	Feb. + Mar.	−0.05	0.04	+0.51	+0.46
Apr. to Oct.....	March	−0.24	0.21	Feb. + Mar.	−0.05	0.04	+0.19	+0.17
May to Oct.....	March	−1.51	1.60	Mar. + Apr.	−3.09	3.27	−1.58	−1.67
May to Oct.....	April	−4.00	4.23	Mar. + Apr.	−3.09	3.27	+0.91	+0.96
June to Oct.....	April	−1.70	2.33	Apr. + May	+0.64	0.88	+1.06	+1.45
June to Oct.....	May	+3.62	4.98	Apr. + May	+0.64	0.88	+2.98	+4.10
July to Oct.....	May	+1.55	2.90	May + June	−0.45	0.84	+1.10	+2.06
July to Oct.....	June	−2.86	5.34	May + June	−0.45	0.84	+2.41	+4.50
Aug. to Oct.....	June	−3.32	9.33	June + July	−3.73	10.48	−0.41	−1.15
Aug. to Oct.....	July	−3.71	10.43	June + July	−3.73	10.48	−0.02	−0.05
Sept. to Oct.....	July	−3.19	16.89	July + Aug.	−3.32	17.60	−0.13	−0.71
Sept. to Oct.....	August	−2.56	13.57	July + Aug.	−3.32	17.60	−0.76	−4.03
October.....	August	−1.10	18.74	Aug. + Sept.	−0.79	13.46	+0.31	+5.28
October.....	September	−0.45	7.67	Aug. + Sept.	−0.79	13.46	−0.34	−5.79

TABLE 6

Average deviation without regard to sign of predicted egg record for a period of months from actual record. Prediction from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Dec. to Oct.....	November	29.59	19.49	—	—	—	—	—
Jan. to Oct.....	November	28.47	19.56	Nov. + Dec.	28.09	19.30	+0.38	+0.26
Jan. to Oct.....	December	28.43	19.53	Nov. + Dec.	28.09	19.30	+0.34	+0.23
Feb. to Oct.....	December	26.92	19.38	Dec. + Jan.	26.25	18.90	+0.67	+0.48
Feb. to Oct.....	January	26.48	19.06	Dec. + Jan.	26.25	18.90	+0.23	+0.16
Mar. to Oct.....	January	25.03	19.40	Jan. + Feb.	24.98	19.37	+0.05	+0.03
Mar. to Oct.....	February	24.07	18.66	Jan. + Feb.	24.98	19.37	−0.91	−0.71
Apr. to Oct.....	February	22.93	20.46	Feb. + Mar.	22.39	19.98	+0.54	+0.48
Apr. to Oct.....	March	22.81	20.36	Feb. + Mar.	22.39	19.98	+0.42	+0.38
May to Oct.....	March	21.78	23.03	Mar. + Apr.	21.31	22.54	+0.47	+0.49
May to Oct.....	April	21.36	22.59	Mar. + Apr.	21.31	22.54	+0.05	+0.05
June to Oct.....	April	20.22	27.80	Apr. + May	19.65	27.02	+0.57	+0.78
June to Oct.....	May	19.89	27.35	Apr. + May	19.65	27.02	+0.24	+0.33
July to Oct.....	May	18.09	33.79	May + June	17.30	32.31	+0.79	+1.48
July to Oct.....	June	17.62	32.91	May + June	17.30	32.31	+0.32	+0.60
Aug. to Oct.....	June	14.88	41.82	June + July	14.05	39.49	+0.83	+2.33
Aug. to Oct.....	July	13.91	39.09	June + July	14.05	39.49	−0.14	−0.40
Sept. to Oct.....	July	10.92	57.90	July + Aug.	10.36	54.93	+0.56	+2.97
Sept. to Oct.....	August	9.76	51.75	July + Aug.	10.36	54.93	−0.60	−3.18
October.....	August	5.67	96.59	Aug. + Sept.	5.13	87.39	+0.54	+9.20
October.....	September	4.57	77.85	Aug. + Sept.	5.13	87.39	−0.56	−9.54

TABLE 7

Square root of mean square deviation of predicted egg record for a period of months from actual record. Prediction from one- and from two-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM TWO MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Dec. to Oct.....	November	38.65	25.46	—	—	—	—	—
Jan. to Oct.....	November	37.05	25.45	Nov. + Dec.	36.46	25.05	+0.59	+0.40
Jan. to Oct.....	December	36.63	25.16	Nov. + Dec.	36.46	25.05	+0.17	+0.11
Feb. to Oct.....	December	34.94	25.15	Dec. + Jan.	34.15	24.58	+0.79	+0.57
Feb. to Oct.....	January	34.61	24.91	Dec. + Jan.	34.15	24.58	+0.46	+0.33
Mar. to Oct.....	January	32.52	25.22	Jan. + Feb.	32.28	25.03	+0.24	+0.19
Mar. to Oct.....	February	30.86	23.92	Jan. + Feb.	32.28	25.03	−1.42	−1.11
Apr. to Oct.....	February	29.17	26.03	Feb. + Mar.	28.12	25.09	+1.05	+0.94
Apr. to Oct.....	March	28.40	25.34	Feb. + Mar.	28.12	25.09	+0.28	+0.25
May to Oct.....	March	27.09	28.65	Mar. + Apr.	26.51	28.03	+0.58	+0.62
May to Oct.....	April	26.50	28.02	Mar. + Apr.	26.51	28.03	−0.01	−0.01
June to Oct.....	April	25.02	34.40	Apr. + May	24.48	33.66	+0.54	+0.74
June to Oct.....	May	24.81	34.11	Apr. + May	24.48	33.66	+0.33	+0.45
July to Oct.....	May	22.34	41.72	May + June	21.24	39.67	+1.10	+2.05
July to Oct.....	June	21.44	40.04	May + June	21.24	39.67	+0.20	+0.37
Aug. to Oct.....	June	18.18	51.09	June + July	17.40	48.90	+0.78	+2.19
Aug. to Oct.....	July	17.14	48.17	June + July	17.40	48.90	−0.26	−0.73
Sept. to Oct.....	July	13.21	70.02	July + Aug.	12.67	67.18	+0.54	+2.84
Sept. to Oct.....	August	12.12	64.26	July + Aug.	12.67	67.18	−0.55	−2.92
October.....	August	6.92	117.84	Aug. + Sept.	6.24	106.30	+0.68	+11.54
October.....	September	5.71	97.27	Aug. + Sept.	6.24	106.30	−0.53	−9.03

with regard to sign are small. No one of the errors is over 4 eggs. The percentage values, in which the actual average yields of the remaining months in question are used as bases, range from 0.2 for the prediction of January-to-October production from December production to 13.6 percent in the case of the prediction of September-to-October production from the August record. The average deviations without regard to sign range from 4.6 to 29.6 eggs. The percentage values range from 18.7 to 77.9 percent of the actual production for the given remaining period.

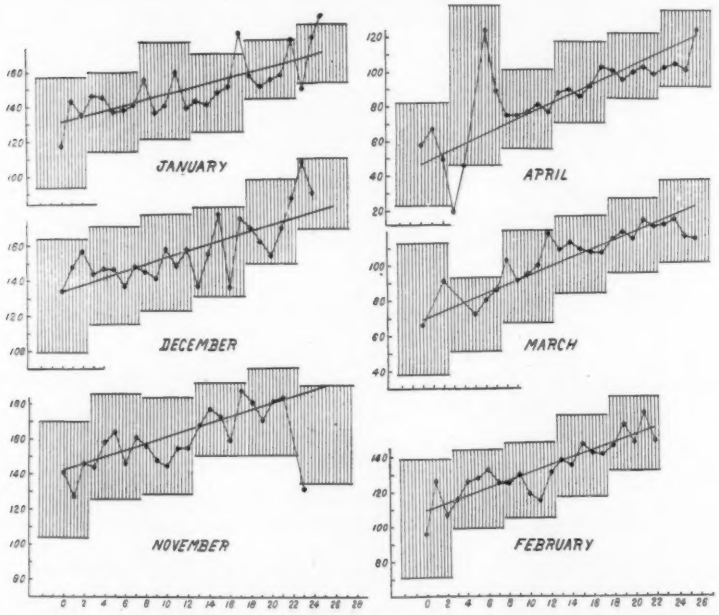

DIAGRAM 3.—Tests of prediction of production for a group of remaining months from single-month records. Tests for November to April. For explanation see text.

The square root of mean square deviations vary from 5.7 to 38.7 eggs, or from 23.9 to 97.3 percent of the actual yield.

The values of the average deviation without regard to sign and of square root of mean square deviation decrease from the earlier to the later months. This is, of course, due to the fact that in predicting the egg record of the remaining months of the year the total record decreases as the number of remaining months becomes smaller. It is to be expected

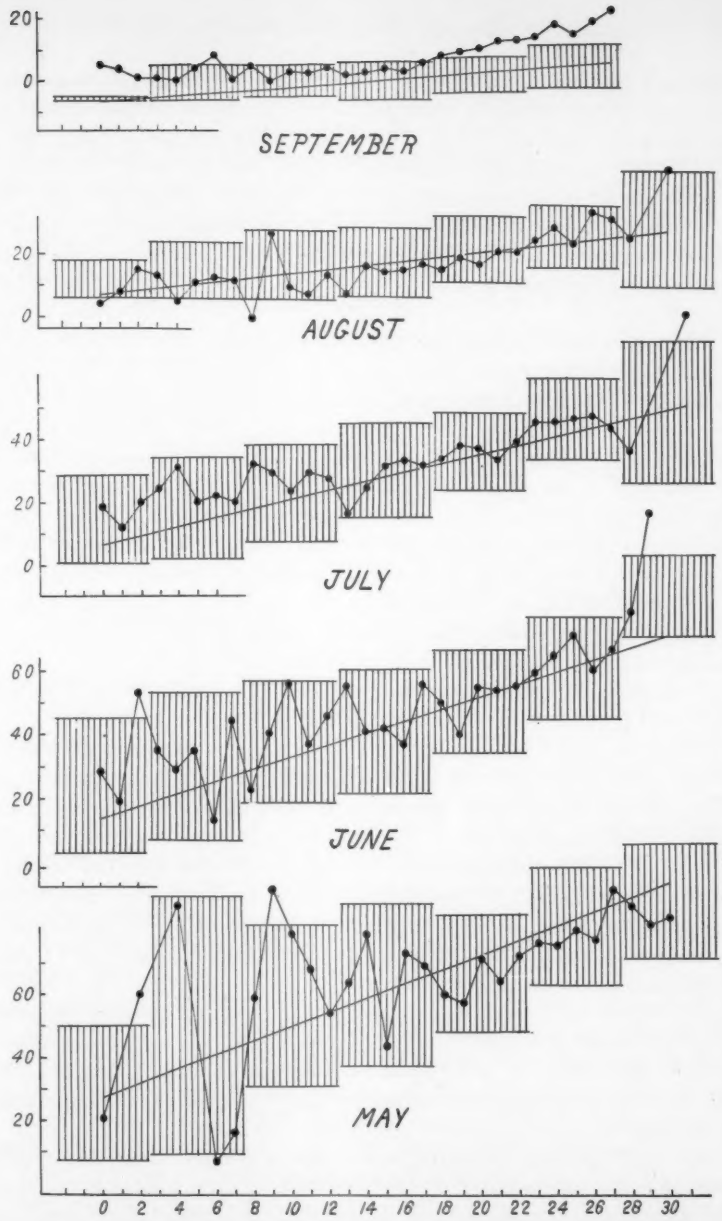

DIAGRAM 4.—Tests of prediction of the production of a group of remaining months from single-month production. Tests for May to September.

therefore, that the absolute error of prediction will be smaller than when the prediction is made for a longer period. The relative errors of prediction are conspicuously larger than those found when the prediction is made for the year as a whole. Furthermore, these relative (percentage) errors increase as the period for which prediction is made becomes shorter. The test shows clearly that prediction of the results of short remaining periods cannot be made,—at least by means of the linear equations for prediction from one month's record tested in this paper,—with a satisfactory degree of accuracy.

When prediction is made for the period subsequent to the $(p + 1)$th month the average deviations with regard to sign vary from 0.56 to 3.32 or from 0.50 to 18.74 percent of the actual production for the period. The average deviations without regard to sign vary from 28.47 eggs for the prediction of January-to-October production from November production to 5.67 eggs for the prediction of October production from August record. The percentage values range from 19.38 to 96.59 percent. Similar results are found in the case of the square root of mean square deviation which ranges from 37.05 eggs for the prediction of January-to-October production from November record to 6.92 eggs for the prediction of October production from August record. The percentage values range from 25.2 to 117.8 percent of the actual records.

The graphic representation of the errors of the prediction of the remaining months of the year is made in diagrams 3 and 4.

The slope of the lines and the moderate narrowness of the shaded areas as well as the fair agreement of the empirical and the predicted means for the remaining periods, evidence for fairly satisfactory prediction for the first six months of the year. As the end of the year is approached and as the period of remaining months becomes shorter the slopes of the lines are more moderate. The narrowness of the shaded areas, representing the difference between the averages of the errors of over-prediction and under-prediction, does not indicate great accuracy of prediction as compared with that attainable in the earlier months, but merely that (because of the smaller egg record made by birds in the latter months of the year) great deviations from prediction are improbable. It is evident, therefore, that for the prediction of the record of the later months of the year from the record of immediately preceding months the equations have relatively little value.

It is quite clear that while the prediction of a group of remaining months may be made with a relatively high degree of accuracy early in the year, the predictions are relatively poor toward the end of the year.

Prediction of annual production from the sum of two monthly records

Before considering the results of equations for the prediction of annual production from the combined record of two or more months, some general questions of theory must be considered.

If the egg production of each individual month be correlated with that of the whole year it would seem that a better prediction of the annual total may be made from the record of two or more individual monthly records than from one month's record only. This is a point emphasized by CARD (1917) who has correlated the total production of groups of months with the annual yield.

There are several points to be taken into consideration here. First, it should be clear that the superiority of a group of months for predicting the annual yield of a bird is to a considerable extent due to the fact that the records of these months are included in the annual total. Thus in predicting annual total from November performance, the November record is included in the annual total. In predicting from November, December and January production the records of these *three* months are included in the annual total. As far as their own contribution is concerned, prediction can be made with absolute certainty. The importance of this factor would be especially great during the spring months when the number of eggs laid by practically all birds is high. If the principle of an increase in the number of months upon which prediction is to be based be extended to its limit, it is clear that the annual total can be predicted with exactness from the record of twelve months. The importance of this factor was fully recognized in our second publication (HARRIS, BLAKESLEE and KIRKPATRICK 1918), in which we determined the correlation between the production of each individual month and that of the remaining eleven months of the year, as well as that between the production of the individual months and the annual record.

It is evident that it is impossible to compare directly and critically the errors made in predicting annual egg production from two-month periods and from single-month periods; in one case a single component only is included in the first and second variable of the pair whereas in the second case two components are involved. The problem of a direct comparison will be taken up in a subsequent section.

Second, from the economic standpoint it is clear that trap-nesting for two months or three months is (disregarding initial investment) twice or three times as expensive as trap-nesting for one month. In general it is important to utilize the shortest practicable period on which prediction may be based.

Third, the mathematical theory of multiple correlation shows that in dealing with correlated characters the gain in accuracy of prediction rapidly decreases with the number of characters employed. In our first detailed treatment of the problem of the correlation between the egg records of the individual months we showed by the constants for a series of selected months that the egg records of the individual months are correlated among themselves. This has since been demonstrated for the entire series of $\frac{1}{2}\ n(n-1) = 66$ different combinations of the 12 months of the pullet year. It is evident, therefore, that very large gains in accuracy of prediction cannot be expected to result from an increase in the number of periods, except in so far as the gain is due directly to the contribution of the months included.

We now turn to the results of the test of equations for the prediction of annual record from two-consecutive-months production. The equations are as follows:

Months from which prediction is made	*Prediction equation*
November and December	$E = +132.887 + 2.160\ (e_1 + e_2)$
December and January	$E = +130.822 + 2.176\ (e_2 + e_3)$
January and February	$E = +146.040 + 2.579\ (e_3 + e_4)$
February and March	$E = +78.008 + 2.915\ (e_4 + e_5)$
March and April	$E = +48.374 + 3.029\ (e_5 + e_6)$
April and May	$E = +39.955 + 3.005\ (e_6 + e_7)$
May and June	$E = +32.783 + 3.065\ (e_7 + e_8)$
June and July	$E = +44.650 + 2.864\ (e_8 + e_9)$
July and August	$E = +62.861 + 2.625\ (e_9 + e_{10})$
August and September	$E = +91.865 + 2.302\ (e_{10} + e_{11})$
September and October	$E = +122.597 + 2.140\ (e_{11} + e_{12})$

Since a primary object of the present analyses is a comparison of equations based on two-months production with those based on a single month's record as a means of predicting the annual egg record of a bird, it is advantageous to place the results for the two methods side by side in the same tables. The results are given in tables 2 to 4.[6]

Table 2 shows the average errors with regard to sign of the egg records of the 415 White Leghorns studied at Storrs in 1917–1918, when prediction is made from two-months production using equations based on the Storrs experience of the preceding six years.

The average deviations with regard to sign are small. In 7 cases the equations have predicted values which are too large, whereas in 4 cases they have predicted values which are too small. The individual errors

[6] It has seemed conducive to clearness to duplicate entries in order to secure the 22 differences which serve as a basis of comparison.

are very small. Two are less than 1 egg, 4 are less than 2 eggs, while 5 are from 2 to 7 eggs. The percentage errors based on the mean annual production are less than 1 percent in 5 of the cases and less than 5 percent

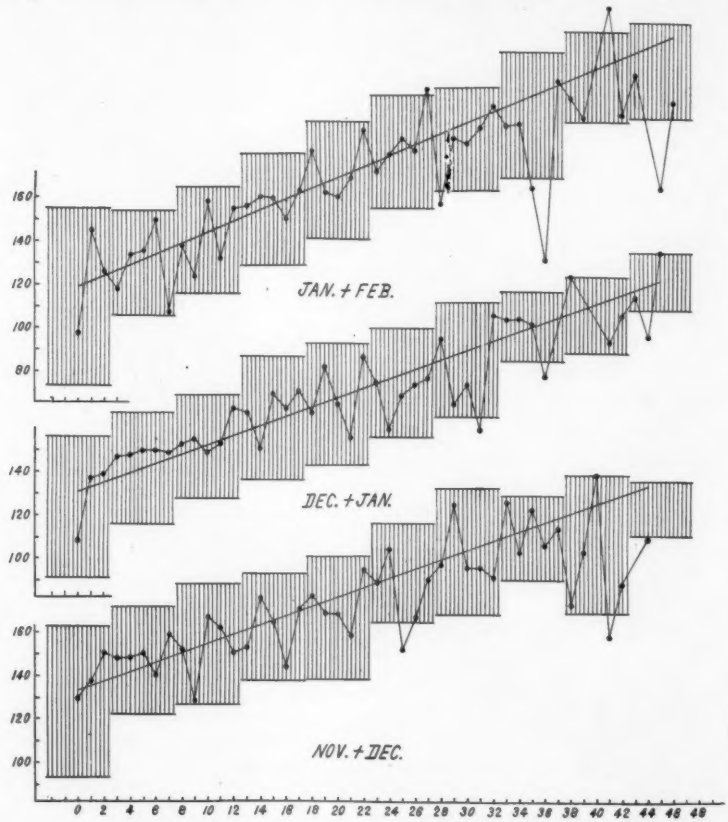

DIAGRAM 5.—Tests of prediction of annual production from combined record of two consecutive months. For explanation see text. Tests for November to February.

in the other 6 cases. The average error in actual number of eggs, disregarding the sign of the error, is 2.72 eggs while the average of percentage errors is 1.72 percent.

It seems unnecessary to discuss in detail the average deviations without regard to sign, of the predicted from the observed annual egg production.

The errors, shown in table 3, range from 23.2 to 28.1 eggs or from 14.7 to 17.8 percent.

Similar results for the square root of mean square deviation are given in table 4 which shows that prediction from the sum of two-consecutive-

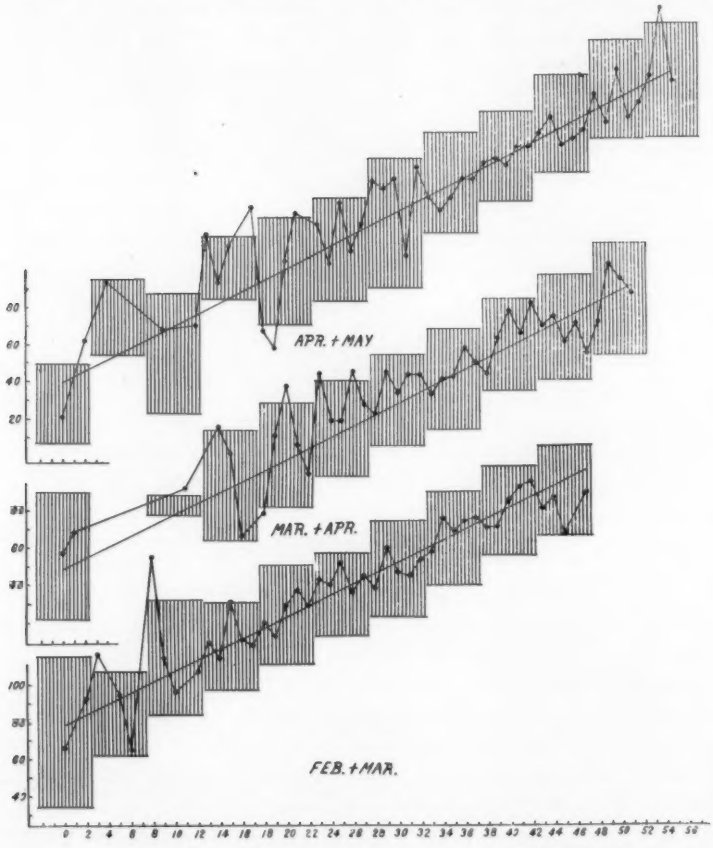

DIAGRAM 6.—Tests of prediction of annual production from the combined record of two consecutive months. Tests of February-to-May production.

months production gives a square root of mean square deviation ranging from 30.4 to 36.5 eggs or from 19.3 to 23.1 percent of the annual production.

Thus it is clear that the annual egg record of a bird may be predicted with a high degree of accuracy from the combined egg record of any two consecutive months.

These results may be represented graphically by diagrams 5–8, which have been prepared on the same principle as those for the results of prediction from a single month's production. The general excellence of the agreement (considering the fact that there are only 415 birds upon which equa-

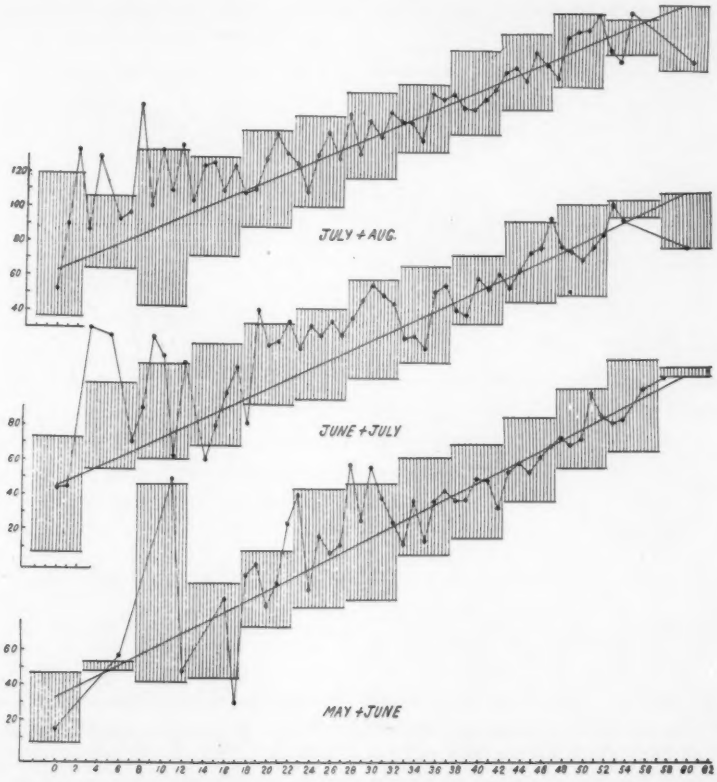

DIAGRAM 7.—Tests of the prediction of annual production from the combined record of two consecutive months. Tests for May to August.

tions based upon an entirely different series are being tested) renders detailed discussion of these diagrams superfluous.

The most interesting feature of these tables is, however, the comparison between the value of two-months observation and of single-month observation as bases for the estimation of the total (annual) egg-producing capacity of the organism.

The differences in the average deviations with regard to sign, as shown in the first of the two final columns of table 2, range from less than a single egg (5 comparisons) to a maximum of less than 7 eggs. The average difference is 2.21 eggs. If signs be considered the average difference is only + 0.67 eggs. The differences in the percentage deviation when prediction is made by single- and by two-month periods are shown in the final column of the table.

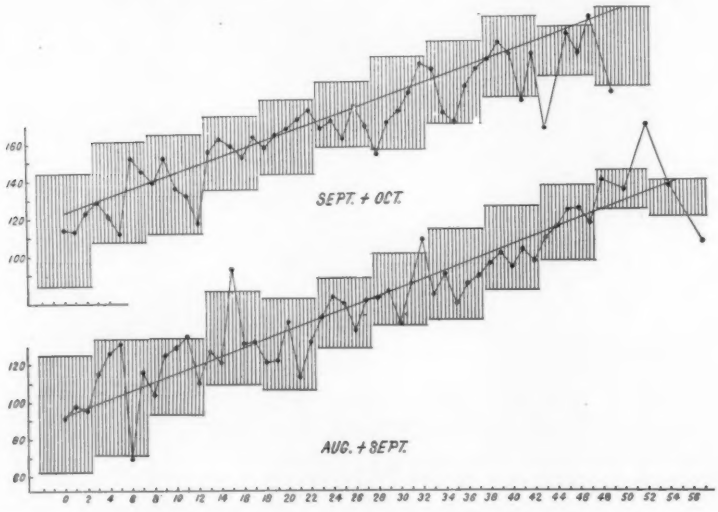

DIAGRAM 8.—Tests of prediction of annual production from the combined record of two consecutive months. Tests of August to October.

It is clear from these results that the results of prediction from two-months production are not materially better from the practical standpoint than those for single-month's production although the labor entailed in recording the performance of a bird for two months must be approximately twice as great as that for a single month.

The reader who cares to do so may verify these statements by a study of the results for average deviation without regard to sign and for square root of mean square deviation as shown in the two final columns of tables 3 and 4.

Prediction of the production of a group of remaining months from the sum of two monthly records

We now have to consider the problem of the accuracy with which the egg production of a group of subsequent months may be predicted from the sum of two consecutive monthly records.

The equations are the following:

Period from which prediction is made	*Period for which prediction is made*	*Prediction equation*
November and December	January to October	$E = +132.887 + 1.160\ (e_1 + e_2)$
December and January	February to October	$E = +128.112 + 0.979\ (e_2 + e_3)$
January and February	March to October	$E = +124.959 + 0.336\ (e_3 + e_4)$
February and March	April to October	$E = +76.542 + 1.320\ (e_4 + e_5)$
March and April	May to October	$E = +44.586 + 1.363\ (e_5 + e_6)$
April and May	June to October	$E = +25.022 + 1.231\ (e_6 + e_7)$
May and June	July to October	$E = +7.280 + 1.118\ (e_7 + e_8)$
June and July	August to October	$E = +0.994 + 0.827\ (e_8 + e_9)$
July and August	September to October	$E = -7.281 + 0.660\ (e_9 + e_{10})$
August and September	October	$E = -2.137 + 0.245\ (e_{10} + e_{11})$

The results appear in the second section of tables 5 to 7. Here they are laid beside the errors obtained for the prediction of the production of these same periods from the record of the two months individually considered, as given by the equations shown on page 282.

Table 5, giving the average deviation with regard to sign of the predicted from the observed values, shows that the actual deviations have a numerical range of 0.05 to 3.73 eggs or from 0.04 to 17.6 percent. The largest relative (percentage) deviations are, of course, in the final months of the year.

The average deviations without regard to sign appear in the second column of table 6. These vary from as low as 5.13 eggs in October to 28.09 eggs for the period January to October. Since the average production decreases as the number of remaining months becomes smaller we find the largest percentage errors in the later groups of months. These percentage values range from 18.9 for the period February to October to 87.4 for the month of October. Similar results with somewhat different numerical values are found in table 7 which shows the square root of mean square deviation of the predicted from the observed values.

These results show that when the number of remaining months is large, prediction of egg production can be made with relatively high accuracy from the combined record of two months. As the number of months becomes smaller the error of prediction is, as compared with the average production, relatively large.

Turning now to the problem of the comparison of periods of one month and of two months as bases of prediction, and testing the efficiency of these two periods on the egg production of comparable remaining periods of time, we note that the differences in the two final columns of tables 5 to 7, expressed either in number of eggs or in percentages of the total production, are small. Thus the differences for the average deviation with regard to sign are all less than 3 eggs and all less than 6 percent. Most of the differences are far smaller than this. In some cases the prediction from a single month gives the better result; in others prediction from two months gives the better result. The differences in the errors without regard to sign as obtained by the two methods are even smaller. No difference amounts to as much as a single egg per year. The large differences in the percentage errors by the two methods are found exclusively in the later months of the year where the total production is low. Comparable, but numerically somewhat different, results are found for the square root of mean square deviation.

Thus it is clear that there is little practical difference between single-month and two-months production as bases of the prediction of the egg record of a subsequent period.

Prediction of annual production from the sum of three monthly records

The equations required for the prediction of annual production from the combined record of three consecutive months are the following:

Months from which prediction is made	*Prediction equation*
November, December and January	$E = +126.742 + 1.770\ (e_1 + e_2 + e_3)$
December, January and February	$E = +113.940 + 1.951\ (e_2 + e_3 + e_4)$
January, February and March	$E = +82.129 + 2.266\ (e_3 + e_4 + e_5)$
February, March and April	$E = +50.502 + 2.323\ (e_4 + e_5 + e_6)$
March, April and May	$E = +29.450 + 2.267\ (e_5 + e_6 + e_7)$
April, May and June	$E = +19.349 + 2.324\ (e_6 + e_7 + e_8)$
May, June and July	$E = +23.786 + 2.233\ (e_7 + e_8 + e_9)$
June, July and August	$E = +41.079 + 2.065\ (e_8 + e_9 + e_{10})$
July, August and September	$E = +67.078 + 1.895\ (e_9 + e_{10} + e_{11})$
August, September and October	$E = +97.699 + 1.794\ (e_{10} + e_{11} + e_{12})$

The second section of table 8 shows the average deviation with regard to sign of the annual egg production predicted from the combined record of 3 consecutive months from the performance of the 415 White Leghorn birds studied at Storrs in 1917–1918.

The results show that the trimonthly totals, like the monthly records and bimonthly totals considered in preceding sections, give excellent predictions. December to February, January to March, March to May, and

July to September give average errors of prediction of less than 1 egg. November to January, April to June, and May to July give errors of prediction of between 2 and 3 eggs. August to October gives an error of predic-

TABLE 8

Average deviation with regard to sign of predicted annual egg record from actual record. Prediction of annual production from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	+2.39	1.52	Nov.–Jan.	+2.09	1.33	+0.30	+0.19
	December	−0.49	0.31	Nov.–Jan.	+2.09	1.33	−1.60	−1.02
	January	+2.58	1.64	Nov.–Jan.	+2.09	1.33	+0.49	+0.31
	December	−0.49	0.31	Dec.–Feb.	+0.78	0.49	−0.29	−0.18
	January	+2.58	1.64	Dec.–Feb.	+0.78	0.49	+1.80	+1.15
	February	+0.06	0.04	Dec.–Feb.	+0.78	0.49	−0.72	−0.45
	January	+2.58	1.64	Jan.–Mar.	+0.49	0.31	+2.09	+1.33
	February	+0.06	0.04	Jan.–Mar.	+0.49	0.31	−0.43	−0.27
	March	−1.63	1.03	Jan.–Mar.	+0.49	0.31	+1.14	+0.72
	February	+0.06	0.04	Feb.–Apr.	−4.07	2.58	−4.01	−2.54
	March	−1.63	1.03	Feb.–Apr.	−4.07	2.58	−2.44	−1.55
	April	−6.23	3.95	Feb.–Apr.	−4.07	2.58	+2.16	+1.37
	March	−1.63	1.03	Mar.–May	−0.73	0.46	+0.90	+0.57
	April	−6.23	3.95	Mar.–May	−0.73	0.46	+5.50	+3.49
	May	+7.02	4.45	Mar.–May	−0.73	0.46	+6.29	+3.99
	April	−6.23	3.95	Apr.–June	−2.31	1.47	+3.92	+2.48
	May	+7.02	4.45	Apr.–June	−2.31	1.47	+4.71	+2.98
	June	−5.21	3.31	Apr.–June	−2.31	1.47	+2.90	+1.84
	May	+7.02	4.45	May–July	−2.12	1.35	+4.90	+3.10
	June	−5.21	3.31	May–July	−2.12	1.35	+3.09	+1.96
	July	−5.27	3.34	May–July	−2.12	1.35	+3.15	+1.99
	June	−5.21	3.31	June–Aug.	−5.35	3.39	−0.14	−0.08
	July	−5.27	3.34	June–Aug.	−5.35	3.39	−0.08	−0.05
	August	−0.82	0.52	June–Aug.	−5.35	3.39	−4.53	−2.87
	July	−5.27	3.34	July–Sept.	−0.20	0.13	+5.07	+3.21
	August	−0.82	0.52	July–Sept.	−0.20	0.13	+0.62	+0.39
	September	+4.78	3.03	July–Sept.	−0.20	0.13	+4.58	+2.90
	August	−0.82	0.52	Aug.–Oct.	+3.91	2.48	−3.09	−1.96
	September	+4.78	3.03	Aug.–Oct.	+3.91	2.48	+0.87	+0.55
	October	+3.95	2.51	Aug.–Oct.	+3.91	2.48	+0.04	+0.03

tion of between 3 and 4 eggs. February to April gives an error of prediction of between 4 and 5 eggs. Finally June to August gives an error of prediction of between 5 and 6 eggs.

Considered in their relation to the average annual production these values range from 0.13 to 3.39 percent. These results certainly show remarkable accuracy of prediction.

The average errors without regard to sign, given in table 9 need not be considered in detail. They range from 21.4 to 25.9 eggs per year or from 13.6 to 16.5 percent of the annual total.

TABLE 9

Average deviation without regard to sign of predicted annual egg record from actual record. Prediction of annual production from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	29.59	18.78	Nov.–Jan.	25.93	16.45	+3.66	+2.33
	December	29.26	18.57	Nov.–Jan.	25.93	16.45	+3.33	+2.12
	January	30.09	19.09	Nov.–Jan.	25.93	16.45	+4.16	+2.64
	December	29.26	18.57	Dec.–Feb.	25.31	16.06	+3.95	+2.51
	January	30.09	19.09	Dec.–Feb.	25.31	16.06	+4.78	+3.03
	February	27.28	17.31	Dec.–Feb.	25.31	16.06	+1.97	+1.25
	January	30.09	19.09	Jan.–Mar.	25.29	16.05	+4.80	+3.04
	February	27.28	17.31	Jan.–Mar.	25.29	16.05	+1.99	+1.26
	March	27.95	17.73	Jan.–Mar.	25.29	16.05	+2.66	+1.68
	February	27.28	17.31	Feb.–Apr.	24.16	15.33	+3.12	+1.98
	March	27.95	17.73	Feb.–Apr.	24.16	15.33	+3.79	+2.40
	April	28.72	18.22	Feb.–Apr.	24.16	15.33	+4.56	+2.89
	March	27.95	17.73	Mar.–May	25.42	16.13	+2.53	+1.60
	April	28.72	18.22	Mar.–May	25.42	16.13	+3.30	+2.09
	May	28.62	18.16	Mar.–May	25.42	16.13	+3.20	+2.03
	April	28.72	18.22	Apr.–June	24.33	15.44	+4.39	+2.78
	May	28.62	18.16	Apr.–June	24.33	15.44	+4.29	+2.72
	June	29.03	18.42	Apr.–June	24.33	15.44	+4.70	+2.98
	May	28.62	18.16	May–July	24.20	15.36	+4.42	+2.80
	June	29.03	18.42	May–July	24.20	15.36	+4.83	+3.06
	July	28.35	17.99	May–July	24.20	15.36	+4.15	+2.63
	June	29.03	18.42	June–Aug.	23.49	14.90	+5.54	+3.52
	July	28.35	17.99	June–Aug.	23.49	14.90	+4.86	+3.09
	August	26.87	17.05	June–Aug.	23.49	14.90	+3.38	+2.15
	July	28.35	17.99	July–Sept.	21.36	13.55	+6.99	+4.44
	August	26.87	17.05	July–Sept.	21.36	13.55	+5.51	+3.50
	September	24.78	15.72	July–Sept.	21.36	13.55	+3.42	+2.17
	August	26.87	17.05	Aug.–Oct.	21.59	13.70	+5.28	+3.35
	September	24.78	15.72	Aug.–Oct.	21.59	13.70	+3.19	+2.02
	October	27.37	17.37	Aug.–Oct.	21.59	13.70	+5.78	+3.67

The square root of mean square deviation of errors of prediction given in table 10 are, of course, larger than the average deviations without regard to sign. They vary from 28.1 to 33.8 eggs or from 17.8 to 21.5 percent of the annual production.

The range of variation in the egg production of three-month periods is so wide that it is impossible because of the limitations of space to represent the errors of prediction from three-month periods graphically for each of the equations.

TABLE 10

Square root of mean square deviation of predicted annual egg record from actual record. Prediction of annual production from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
For the whole year	November	38.65	24.52	Nov.–Jan.	33.84	21.47	+4.81	+3.05
	December	37.61	23.86	Nov.–Jan.	33.84	21.47	+3.77	+2.39
	January	38.77	24.60	Nov.–Jan.	33.84	21.47	+4.93	+3.13
	December	37.61	23.86	Dec.–Feb.	32.65	20.72	+4.96	+3.14
	January	38.77	24.60	Dec.–Feb.	32.65	20.72	+6.12	+3.88
	February	34.70	22.02	Dec.–Feb.	32.65	20.72	+2.05	+1.30
	January	38.77	24.60	Jan. –Mar.	31.58	20.04	+7.19	+4.56
	February	34.70	22.02	Jan. –Mar.	31.58	20.04	+3.12	+1.98
	March	34.28	21.75	Jan. –Mar.	31.58	20.04	+2.70	+1.71
	February	34.70	22.02	Feb. –Apr.	29.77	18.89	+4.93	+3.13
	March	34.28	21.75	Feb –Apr.	29.77	18.89	+4.51	+2.86
	April	35.31	22.40	Feb. –Apr.	29.77	18.89	+5.54	+3.51
	March	34.28	21.75	Mar.–May	31.14	19.76	+3.14	+1.99
	April	35.31	22.40	Mar.–May	31.14	19.76	+4.17	+2.64
	May	35.89	22.77	Mar.–May	31.14	19.76	+4.75	+3.01
	April	35.31	22.40	Apr. –June	30.59	19.41	+4.72	+2.99
	May	35.89	22.77	Apr. –June	30.59	19.41	+5.30	+3.36
	June	36.53	23.18	Apr. –June	30.59	19.41	+5.94	+3.77
	May	35.89	22.77	May–July	29.40	18.65	+6.49	+4.12
	June	36.53	23.18	May–July	29.40	18.65	+7.13	+4.53
	July	35.89	22.77	May–July	29.40	18.65	+6.49	+4.12
	June	36.53	23.18	June–Aug.	29.80	18.91	+6.73	+4.27
	July	35.89	22.77	June–Aug.	29.80	18.91	+6.09	+3.86
	August	34.34	21.79	June–Aug.	29.80	18.91	+4.54	+2.88
	July	35.89	22.77	July –Sept.	28.10	17.83	+7.79	+4.94
	August	34.34	21.79	July –Sept.	28.10	17.83	+6.24	+3.96
	September	32.94	20.90	July Sept.	28.10	17.83	+4.84	+3.07
	August	34.34	21.79	Aug.–Oct.	29.23	18.55	+5.11	+3.24
	September	32.94	20.90	Aug.–Oct.	29.23	18.55	+3.71	+2.35
	October	36.47	23.14	Aug.–Oct.	29.23	18.55	+7.24	+4.59

Two series, that for November to January and for March to May, have been selected at random to represent the goodness of fit of prediction in these cases. The results for prediction from November to January record are shown in diagram 9. Those for prediction from March to May pro-

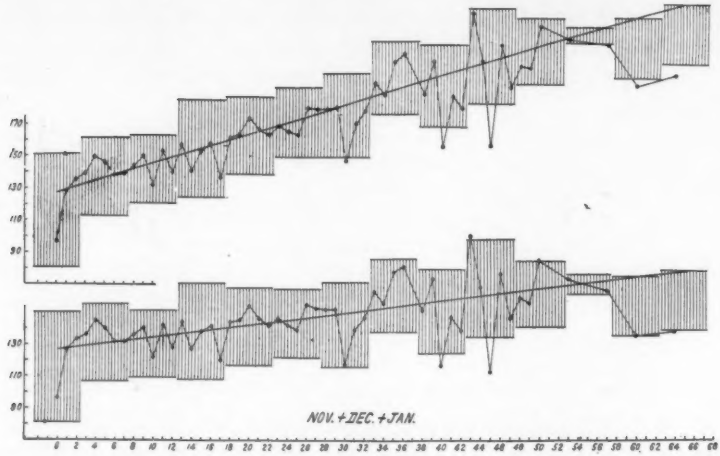

DIAGRAM 9.—Tests of the prediction of annual production (upper figure) and of the production of a group of remaining months (lower figure) from the combined record of three consecutive months. Tests for the period November to January.

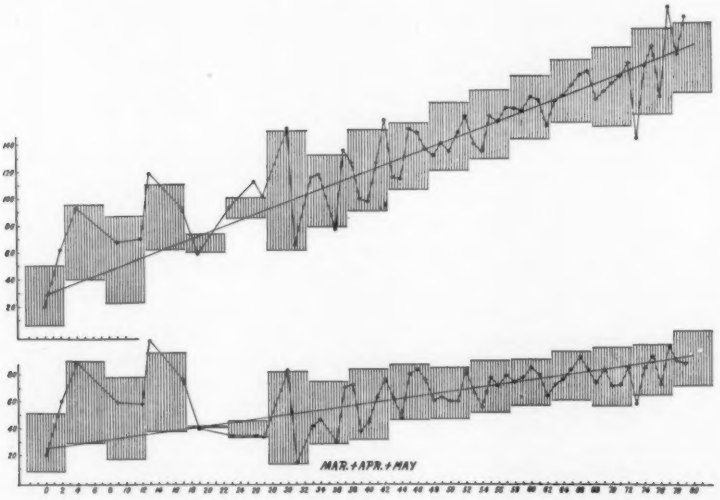

DIAGRAM 10.—Tests of the prediction of annual production (upper figure) and of the production of a group of remaining months (lower figure) from the combined record of three consecutive months. Tests for the period March to May.

duction are shown in diagram 10. In both cases the upper figure represents the prediction of annual production. The lower figure shows the prediction of the groups of remaining months and will be discussed in a subsequent section.

After the discussion of the preceding diagrams these graphs are self-explanatory.

When these results are compared, as in the last two columns of the tables, with those for prediction from a single one of the three months the differences are surprisingly small. For example the most important test,—that of the average deviation with regard to sign,—shows that 11 of the 30 differences are less than 1 egg per year; 3 are less than 2 eggs per year; while 16 are 2 eggs or more per year. In no case is the difference as much as 7 eggs per year. The difference in percentage deviation is in no case as large as 4 percent.

Turning to the comparison of average deviation without regard to sign when prediction is made from trimonthly periods and from the records of individual months we note that the differences are without exception positive in sign. Thus they show a greater error when prediction is made from a single monthly record. The differences are, however, always less than 7 eggs per year and are generally less than 5 eggs. The percentage differences vary from 1.3 to 4.4 percent when both percentages are based on the annual total.

Similar results are obtained for the square root of mean square deviation. The deviations are larger throughout when prediction is made from single-months records than when made from three-months records. The differences are not, however, large. They range from 2.05 to 7.79 eggs, or from 1.30 to 4.94 percent of the annual average production.

Thus while practically without exception a closer prediction of the annual egg record of individual birds can be made from three-months production the difference between a three-month period and a single-month period is by no means so large as one unacquainted with statistical theory might have assumed.

Prediction of the production of a subsequent period from the sum of three monthly records

The equations required are the following:

Months from which prediction is made	*Period for which prediction is made*	*Prediction equation*
November, Dec. and Jan.	February to October	$E_9 = +126.742 + 0.770\ (e_1 + e_2 + e_3)$
Dec., Jan. and Feb.	March to October	$E_8 = +112.051 + 0.806\ (e_2 + e_3 + e_4)$
Jan., Feb. and March	April to October	$E_7 = +81.464 + 0.935\ (e_3 + e_4 + e_5)$
February, March and April	May to October	$E_6 = +49.753 + 0.955\ (e_4 + e_5 + e_6)$
March, April and May	June to October	$E_5 = +25.210 + 0.850\ (e_5 + e_6 + e_7)$
April, May and June	July to October	$E_4 = +7.063 + 0.770\ (e_6 + e_7 + e_8)$
May, June and July	August to October	$E_3 = -1.975 + 0.594\ (e_7 + e_8 + e_9)$
June, July and August	September to October	$E_2 = -4.701 + 0.377\ (e_8 + e_9 + e_{10})$
July, August and September	October	$E_1 = -3.343 + 0.172\ (e_9 + e_{10} + e_{11})$

Table 11 contains the average deviations with regard to sign, of the predicted yield of remaining months, from the actual productions, when prediction is made from the total yield of three consecutive months.

The deviations range from 0.20 to 3.30 eggs or from 0.27 to 18.22 percent of the actually observed yield. As far as this criterion shows, predictions are excellent for all periods from that including February to October to that for August to October. The September-to-October record and the October record, however, cannot be predicted with a high degree of accuracy, the errors being over 17 percent of the mean value for these months.

The average deviations without regard to sign, shown in table 12, range from 5.24 to 25.93 eggs, the values decreasing as the length of the period for which prediction is made becomes smaller. The reverse is true of the percentage values which increase from 18.66 percent for the period February to October to 89.23 percent of the actual yield for the month of October.

Similar results are obtained when the formulae are judged by the square root of mean square deviation of the predicted from the actually observed egg record as shown in table 13. These root mean square deviations range from 33.84 for February to October to 6.44 for the month of October alone, or from 24.30 percent for the group of 8 remaining months of the year to 109.67 percent for the last (single) month.

The results for the prediction of two of the groups of remaining months from the combined records of three-months production are represented graphically for the three months November to January in diagram 9 and for the three months March to May in diagram 10. It is the lower figure which is to be consulted in each case.

The gentle slope of the lines and the considerable irregularities of the means show that prediction of the record of a period of remaining months

TABLE 11

Average deviation with regard to sign of predicted egg record for a period of months from actual record. Prediction from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Feb. to Oct.	November	+2.16	1.55	Nov.–Jan.	+2.09	1.50	+0.07	+0.05
Feb. to Oct.	December	+0.99	0.71	Nov.–Jan.	+2.09	1.50	−1.10	−0.79
Feb. to Oct.	January	+2.37	1.71	Nov.–Jan.	+2.09	1.50	+0.28	+0.21
Mar. to Oct.	December	+0.91	0.71	Dec.–Feb.	+1.35	1.05	−0.44	−0.34
Mar. to Oct.	January	+2.02	1.57	Dec.–Feb.	+1.35	1.05	+0.67	+0.52
Mar. to Oct.	February	+0.99	0.77	Dec.–Feb.	+1.35	1.05	−0.36	−0.28
Apr. to Oct.	January	+1.40	1.25	Jan. –Mar.	+0.73	0.65	+0.67	+0.60
Apr. to Oct.	February	+0.56	0.50	Jan. –Mar.	+0.73	0.65	−0.17	−0.15
Apr. to Oct.	March	−0.24	0.21	Jan. –Mar.	+0.73	0.65	−0.49	−0.44
May to Oct.	February	−0.77	0.81	Feb.–Apr.	−2.51	2.65	−1.74	−1.84
May to Oct.	March	−1.51	1.60	Feb.–Apr.	−2.51	2.65	−1.00	−1.05
May to Oct.	April	−4.00	4.23	Feb.–Apr.	−2.51	2 65	+1.49	+1.58
June to Oct.	March	−0.01	0.01	Mar.–May	+0.20	0.27	−0.19	−0.26
June to Oct.	April	−1.70	2.33	Mar.–May	+0.20	0.27	+1.50	+2.06
June to Oct.	May	+3.62	4.98	Mar.–May	+0.20	0.27	+3.42	+4.71
July to Oct.	April	−2.16	4.03	Apr.–June	−1.49	2.78	+0.67	+1.25
July to Oct.	May	+1.55	2.90	Apr.–June	−1.49	2.78	+0.06	+0.12
July to Oct.	June	−2.86	5.34	Apr.–June	−1.49	2.78	+1.37	+2.56
Aug. to Oct.	May	−0.51	1.43	May–July	−2.56	7.20	−2.05	−5.77
Aug. to Oct.	June	−3.32	9.33	May–July	−2.56	7.20	+0.76	+2.13
Aug. to Oct.	July	−3.71	10.43	May–July	−2.56	7.20	+1.15	+3.23
Sept. to Oct.	June	−3.00	15.91	June–Aug.	−3.30	17.50	−0.30	−1.59
Sept. to Oct.	July	−3.19	16.89	June–Aug.	−3.30	17.50	−0.11	−0.61
Sept. to Oct.	August	−2.56	13.57	June–Aug.	−3.30	17.50	−0.74	−3.93
October	July	−1.33	22.64	July –Sept.	−1.07	18.22	+0.26	+4.42
October	August	−1.10	18.74	July –Sept.	−1.07	18.22	+0.03	+0.52
October	September	−0.45	7.67	July –Sept.	−1.07	18.22	−0.62	−10.55

TABLE 12

Average deviation without regard to sign of predicted egg record for a period of months from actual record. Prediction from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Feb. to Oct.....	November	26.67	19.20	Nov.–Jan.	25.93	18.66	+0.74	+0.54
Feb. to Oct.....	December	26.92	19.38	Nov.–Jan.	25.93	18.66	+0.99	+0.72
Feb. to Oct.....	January	26.48	19.06	Nov.–Jan.	25.93	18.66	+0.55	+0.40
Mar. to Oct.....	December	25.33	19.61	Dec.–Feb.	24.19	18.75	+1.14	+0.86
Mar. to Oct.....	January	25.03	19.40	Dec.–Feb.	24.19	18.75	+0.84	+0.65
Mar. to Oct.....	February	24.07	18.66	Dec.–Feb.	24.19	18.75	−0.12	−0.09
Apr. to Oct.....	January	23.68	21.13	Jan. –Mar.	22.63	20.20	+1.05	+0.93
Apr. to Oct.....	February	22.93	20.46	Jan. –Mar.	22.63	20.20	+0.30	+0.26
Apr. to Oct.....	March	22.81	20.36	Jan. –Mar.	22.63	20.20	+0.18	+0.16
May to Oct.....	February	21.73	22.98	Feb.–Apr.	21.03	22.24	+0.70	+0.74
May to Oct.....	March	21.78	23.03	Feb.–Apr.	21.03	22.24	+0.75	+0.79
May to Oct.....	April	21.36	22.59	Feb.–Apr.	21.03	22.24	+0.33	+0.35
June to Oct.....	March	20.57	28.28	Mar.–May	19.75	27.16	+0.82	+1.12
June to Oct.....	April	20.22	27.80	Mar.–May	19.75	27.16	+0.47	+0.64
June to Oct.....	May	19.89	27.35	Mar.–May	19.75	27.16	+0.14	+0.19
July to Oct.....	April	18.49	34.54	Apr.–June	17.44	32.58	+1.05	+1.96
July to Oct.....	May	18.09	33.79	Apr.–June	17.44	32.58	+0.65	+1.21
July to Oct.....	June	17.62	32.91	Apr.–June	17.44	32.58	+0.18	+0.33
Aug. to Oct.....	May	15.03	42.25	May–July	14.03	39.44	+1.00	+2.81
Aug. to Oct.....	June	14.88	41.83	May–July	14.03	39.44	+0.85	+2.39
Aug. to Oct.....	July	13.91	39.09	May–July	14.03	39.44	−0.12	−0.35
Sept. to Oct.....	June	11.27	59.76	June–Aug.	10.26	54.40	+1.01	+5.36
Sept. to Oct.....	July	10.92	57.90	June–Aug.	10.26	54.40	+0.66	+3.50
Sept. to Oct.....	August	9.76	51.75	June–Aug.	10.26	54.40	−0.50	−2.65
October.....	July	5.76	98.09	July –Sept.	5.24	89.23	+0.52	+8.86
October.....	August	5.67	96.59	July –Sept.	5.24	89.23	+0.43	+7.36
October.....	September	4.57	77.85	July –Sept.	5.24	89.23	−0.67	−11.38

TABLE 13

Square root of mean square deviation of predicted egg record for a period of months from actual record. Prediction from one- and from three-months performance. Equations based on Storrs experience, 1911 to 1917. Test of equations on 415 White Leghorns, Storrs, 1917–1918.

PERIOD FOR WHICH PREDICTION IS MADE	PREDICTION FROM ONE MONTH			PREDICTION FROM THREE MONTHS			DIFFERENCE IN ACTUAL DEVIATION	DIFFERENCE IN PERCENTAGE DEVIATION
	Base of prediction	Actual deviation	Percentage deviation	Base of prediction	Actual deviation	Percentage deviation		
Feb. to Oct.....	November	35.01	25.20	Nov.–Jan.	33.84	24.36	+1.17	+0.84
Feb. to Oct.....	December	34.94	25.15	Nov.–Jan.	33.84	24.36	+1.10	+0.79
Feb. to Oct.....	January	34.61	24.91	Nov.–Jan.	33.84	24.36	+0.77	+0.55
Mar. to Oct.....	December	32.74	25.38	Dec.–Feb.	31.35	24.30	+1.39	+1.08
Mar. to Oct.....	January	32.52	25.22	Dec.–Feb.	31.35	24.30	+1.17	+0.92
Mar. to Oct.....	February	30.86	23.92	Dec.–Feb.	31.35	24.30	−0.49	−0.38
Apr. to Oct.....	January	30.30	27.04	Jan. –Mar.	28.62	25.54	+1.68	+1.50
Apr. to Oct.....	February	29.17	26.03	Jan. –Mar.	28.62	25.54	+0.55	+0.49
Apr. to Oct.....	March	28.40	25.34	Jan. –Mar.	28.62	25.54	−0.22	−0.20
May to Oct.....	February	27.10	28.66	Feb.–Apr.	26.14	27.64	+0.96	+1.02
May to Oct.....	March	27.09	28.65	Feb.–Apr.	26.14	27.64	+0.95	+1.01
May to Oct.....	April	26.50	28.02	Feb.–Apr.	26.14	27.64	+0.36	+0.38
June to Oct.....	March	25.49	35.05	Mar.–May	24.70	33.96	+0.79	+1.09
June to Oct.....	April	25.02	34.40	Mar.–May	24.70	33.96	+0.32	+0.44
June to Oct.....	May	24.81	34.11	Mar.–May	24.70	33.96	+0.11	+0.15
July to Oct.....	April	22.51	42.05	Apr.–June	21.42	40.01	+1.09	+2.04
July to Oct.....	May	22.34	41.72	Apr.–June	21.42	40.01	+0.92	+1.71
July to Oct.....	June	21.44	40.04	Apr.–June	21.42	40.01	+0.02	+0.03
Aug. to Oct.....	May	18.28	51.38	May–July	17.05	47.93	+1.23	+3.45
Aug. to Oct.....	June	18.18	51.09	May–July	17.05	47.93	+1.13	+3.16
Aug. to Oct.....	July	17.14	48.17	May–July	17.05	47.93	+0.09	+0.24
Sept. to Oct.....	June	13.48	71.47	June–Aug.	12.52	66.38	+0.96	+5.09
Sept. to Oct.....	July	13.20	70.00	June–Aug.	12.52	66.38	+0.68	+3.62
Sept. to Oct.....	August	12.12	64.26	June–Aug.	12.52	66.38	−0.40	−2.12
October.....	July	7.06	120.23	July–Sept.	6.44	109.67	+0.62	+10.56
October.....	August	6.92	117.84	July–Sept.	6.44	109.67	+0.48	+8.17
October.....	September	5.71	97.27	July–Sept.	6.44	109.67	−0.73	−12.40

is not so satisfactory as might be desired. Great irregularities are to be expected when a flock of only 415 birds is divided up into such a large number of classes. The results indicate that if applied to larger flocks the prediction equations for the production of a group of remaining months from three-months recorded production might be made with greater precision.

In comparing the error of prediction for a group of subsequent months from three-month periods with the errors of prediction for the same period when prediction is made from single months we require three sets of equations for the prediction of the yields of a group of months from a monthly record. Two sets of these have been given on page 282 and used in comparison with the results of prediction from bimonthly periods.

The additional equations required are:

Month from which prediction is made	*Period for which prediction is made*	*Prediction equation*
November	February to October	$E_9 = +134.546 + 1.143\ e_1$
December	March to October	$E_8 = +122.721 + 1.165\ e_2$
January	April to October	$E_7 = +106.659 + 1.033\ e_3$
February	May to October	$E_6 = +80.512 + 1.342\ e_4$
March	June to October	$E_5 = +47.994 + 1.462\ e_5$
April	July to October	$E_4 = +30.111 + 1.219\ e_6$
May	August to October	$E_3 = +13.094 + 1.008\ e_7$
June	September to October	$E_2 = +3.462 + 0.649\ e_8$
July	October	$E_1 = +0.297 + 0.240\ e_9$

When we compare the results for the prediction of the yield of a group of subsequent months from single monthly records and from trimonthly records of production we find that the differences in errors of prediction are surprisingly small. Specifically we note that in the case of the average deviation with regard to sign, shown in the two last columns of table 11, the differences in actual errors range from 0.03 to 3.42 eggs while the differences in percentage values range from 0.05 to 10.55. In some cases the three-month period gives a numerically larger error of prediction while in other cases the one-month period gives the larger error.

When the comparison is made on the basis of average deviation without regard to sign (table 12) the single-month period gives a slightly larger average deviation in most cases, 23 out of 27 cases. The differences are, however, very small, varying from 0.12 to 1.14 eggs.

Similar results are obtained when the comparisons (between the single component months and the three-months record as bases of prediction) are based upon square root of mean square deviation (table 13). In 23 of the 27 cases prediction from a monthly record gives slightly more variable

errors than prediction from the combined record of three months. The differences are, however, insignificant, varying from 0.02 to 1.68 eggs. It is clear, therefore, that if the linear equation be used for the purpose of predicting the yield of a group of remaining months, about as good results for practical purposes may be obtained from single month records as from the sum of three months records.

It is quite possible that with equations other than the linear this will not be the case. Such equations will be investigated in future work.

Comparison of the two- and three-month periods as bases for the prediction of the egg record of the subsequent months

In the foregoing discussion comparisons between the value of single-month periods and two-month periods and between single-month and three-month periods as bases for prediction have been made. It will be of some interest to compare two- and three-month periods in the same way. Certain of the data may be rearranged from preceding tables. Special calculations would, however, be necessary to complete all of the possible comparisons. It is evident that for a critical comparison between the two groups it is necessary to deal with the egg record of a group of remaining months. Thus in comparing November-to-January production with November-and-December or December-and-January production as bases of prediction it is necessary to determine the accuracy with which the egg production of February to October may be predicted since none of the months included in the base of prediction should also occur in the period for which prediction is made.

Limiting our attention to the comparisons which can be made from the data in the preceding tables[7] we note that in some cases there is a larger average deviation with regard to sign in predicting from two-months and in some cases a larger error in predicting from three-months production.

The same may be shown to be true for the average deviation without regard to sign and for the square root of mean square deviation of the predicted from the actual values. Thus there is little practical advantage in dealing with three-months production as compared with two-months production as bases for the prediction of the record of a group of subsequent months.

[7] The subsidiary tables upon which the following conclusions were based may be formed from tables 5 to 7 and 11 to 13. It seems unnecessary to publish these tables here.

Comparison of the four periods as bases for the prediction of the egg record of the year

In the introductory sections of this paper we called attention to the so-called periods or cycles of egg production which have been recognized by a number of students of fecundity in the domestic fowl. It might at first seem desirable to compare the results of predicting from these periods.

Since these periods are consecutive and together make up the entire laying year it is impossible to obtain any common basis for testing their efficiency such as has been found in periods of subsequent months in preceding tests.

In view of this fact it does not seem desirable in this place to go into the question of the comparison of these conventional periods as bases of prediction. Practically all of the data required for such comparison as can be made appear in the foregoing tables 2 to 13. The reader who desires to do so may abstract the constants from these tables.

SUMMARY AND CONCLUSIONS

The specific purpose of the present paper, which is one of a series dealing with the general problem of variation and correlation of egg production in the domestic fowl, is to consider the possibility of predicting the future egg production or the total annual egg production of White Leghorn birds from the record of an individual month or a group of consecutive months.

The investigation has been carried out because of two convictions: First, factors underlying the distribution, inheritance and interrelationships of fecundity in birds present a problem of first-rate biological importance. Second, that it is one of the functions of the biologist to provide the agricultural economist with the quantitative constants and formulae upon which the scientific agriculture of the future must largely rest.

The method followed has been to determine a series of prediction equations based on the experience of six years (1911 to 1917) of the INTERNATIONAL EGG-LAYING CONTEST at Storrs and to test these equations upon an additional series of 415 birds studied at Storrs in 1917–1918. Thus the equations have been tested upon a different series of birds from that upon which they were based, but upon birds maintained under conditions comparable with those upon whose record the fundamental equations were based.

The results show that the annual egg record of a series of birds may be predicted with a reasonably high degree of accuracy when their performance for a single month is known. Somewhat higher accuracy may be obtained

when the record of two or more months is taken into consideration, but the improvement due to an increase in the number of months upon which prediction is based is not great.

Prediction of the egg record which will be made by groups of birds subsequently to the month or group of months chosen as a basis of prediction can also be made, but the accuracy of prediction decreases rapidly as the period for which prediction is made becomes shorter.

The results show that in the case of a flock of White Leghorn fowl, which is essentially identical in genetic composition and maintained under essentially uniform conditions from year to year, it is quite possible to estimate annual egg production from the record of either a single month or of two or three consecutive months with a high degree of accuracy. The same is presumably true of other breeds as well. This point is now under investigation.

It is probably not feasible to use the equations given in this paper for flocks differing greatly in genetic composition or in conditions of maintenance from that upon which these equations were based. The problem of the determination of corrective terms by which the equations may be applied to flocks other than that upon which they are based is now under investigation.

LITERATURE CITED

ALDER, B., and EGBERT, A. D., 1918 A quick method of obtaining individual egg records without the trap nest. Bull. Utah Agric. Exp. Sta. 162.

BLAKESLEE, A. F., HARRIS, J. ARTHUR, WARNER, D. E., and KIRKPATRICK, W. F., 1917 Pigmentation and other criteria for the selection of laying hens. Bull. Storrs Agric. Exp. Sta. 92, pp. 95–194.

CARD, L. E., 1917 A study of egg production in the White Leghorns. Bull. Storrs Agric. Exp. Sta. 91, pp. 41–90.

HARRIS, J. ARTHUR, BLAKESLEE, A. F., and WARNER, D. E., 1917 Body pigmentation and egg production in the fowl. Proc. Nation. Acad. Sci. 3: 237–241. *Fig. 1–3.*

HARRIS, J. ARTHUR, BLAKESLEE, A. F., and KIRKPATRICK, W. F., 1917 Interperiodic correlation in the egg production of the domestic fowl. Proc. Nation. Acad. Sci. 3: 565–569. *Fig. 1–2.*

HARRIS, J. ARTHUR. BLAKESLEE, A. F., and KIRKPATRICK, W. F., 1918 The correlation between egg production during various periods of the year in the domestic fowl. Genetics 3: 27–72. *Fig. 1–11.*

HARRIS, J. ARTHUR, BLAKESLEE, A. F., WARNER, D. E., and KIRKPATRICK, W. F., 1917 The correlation between body pigmentation and egg production in the domestic fowl. Genetics 2: 36–77. *Fig. 1–16.*